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TULANE STUDIES IN ZOOLOGY AND BOTANY

VOLUME 16
1969-1970



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Price per number (flat rate): \$1.50

Price per volume (flat rate): \$5.00

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Volume 16, Number 1

December 16, 1969

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VARIATION AND RELATIONSHIP OF THE STUDFISHES,
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(CYPRINODONTIDAE, PISCES)

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BAIRD AND GIRARD

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SATYU YAMAGUTI AND SHUNYA KAMEGAI

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FUNDULUS CATENATUS AND *FUNDULUS STELLIFER*
(CYPRINODONTIDAE, PISCES)

JAMIE E. THOMERSON

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ABSTRACT

Fundulus catenatus and *Fundulus stellifer* are recognized as valid allopatric (with the exception of a problematic syntopic record) species differing in pigmentation, male breeding coloration, distribution of male contact organs and pharyngeal dentition. On the basis of meristic and morphometric differences eight populations (Ozarks, Ouachita, Homochitto River, Tennessee R., Virginia, Cumberland R., Green R. and Indiana) of *F. catenatus* and six populations (Upper Coosa R., Middle Coosa R., Alabama R., Cahaba R., Tallapoosa R. and Chattahoochee R.) of *F. stellifer* are recognized. The Homochitto population seems to be dwarfed and no black-banded males were recorded. In both species, males occur in two breeding color forms: those with and those without a black band on the caudal fin. *Fundulus stellifer* males with the black caudal band have black terminal dorsal bands also. The black caudal band is usually subterminal in *F. catenatus* and terminal in *F. stellifer* males. The more massive pharyngeal bones and teeth of *F. stellifer* are regarded as evidence for further specialization for snail feeding. *Fundulus catenatus* probably originated in the Eastern Highlands and the Ozarks and Ouachita populations may be the result of separate invasions of the Interior Highlands. *Fundulus stellifer* was derived from a *F. catenatus*-like ancestor isolated in the Alabama River system by minor stream capture.

INTRODUCTION

The northern studfish, *Fundulus catenatus* (Storer) 1846, is a large active killifish which

inhabits the clear sand and gravel bottom streams draining the upland areas of the central United States. It is known only from streams ultimately tributary to the Mississippi River and is one of a number of animal species distributed disjunctly in the Interior Highlands of Missouri and Arkansas west of the Mississippi River and in the Cumberland and Appalachian uplands east of the Mississippi River (see Conant, 1960, for a discussion of this distributional pattern). With the exception of an isolated population in the Homochitto River drainage in Mississippi, *F. catenatus* is absent from the intervening Mississippi Embayment of the Gulf Coastal Plain to the south and the predominantly prairie state of Illinois to the north. *Fundulus stellifer* (Jordan) 1876, the southern studfish, has its main distribution in the upland tributaries of the Alabama River in Alabama and Georgia and few of the headwater tributaries of the Chattahoochee River in northern Georgia. With the exception of a single problematic syntopic record discussed below, the two studfishes appear to be completely allopatric. Though extensive comparative life history data are not yet available, they occupy similar habitats and *F. stellifer* may be thought of as replacing *F. catenatus* in its range.

The studfishes are quite similar morphologically (Figure 1) and were even considered conspecific by Garman (1895, pp. 107-108), but presently (Moore, 1968;

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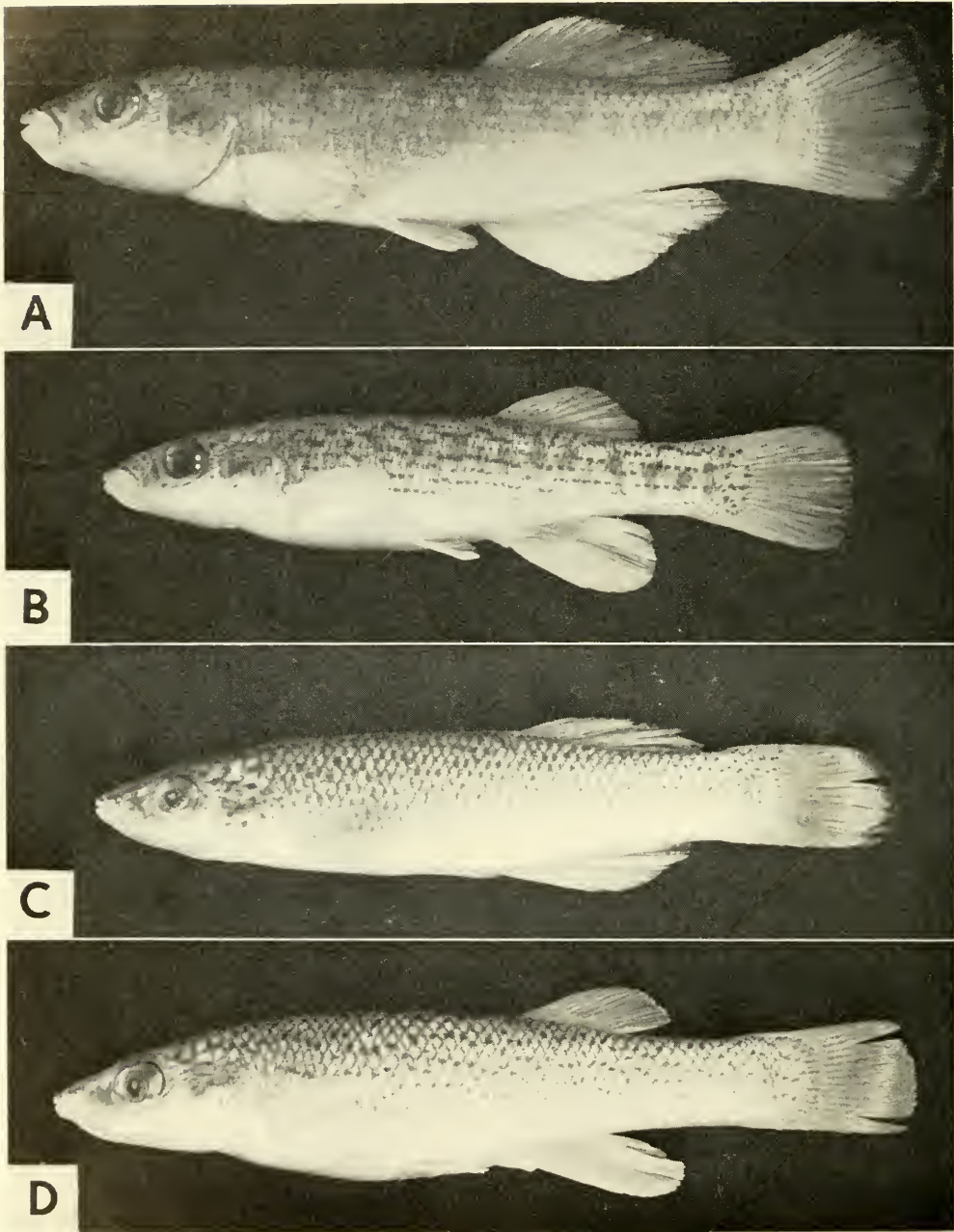


Figure 1. A. Male *Fundulus catenatus* (SL 86.6 mm), and B. female *F. catenatus* (SL 69.4 mm) from SIUE collection JET 66-10, Ozarks Population. C. Male *Fundulus stellifer* (SL 68.5 mm), and D. female *F. stellifer* (SL 68.8 mm) from TU 37703, Cahaba River Population.

Bailey, *et al.*, 1960) they are considered distinct species. However, Miller (1955) has reasonably suggested that further study might show them to be subspecies rather than allo-

patric species. The purpose of this study is to describe and compare variation in the two forms and to clarify their relationship. The problem is simplified in that the studfishes

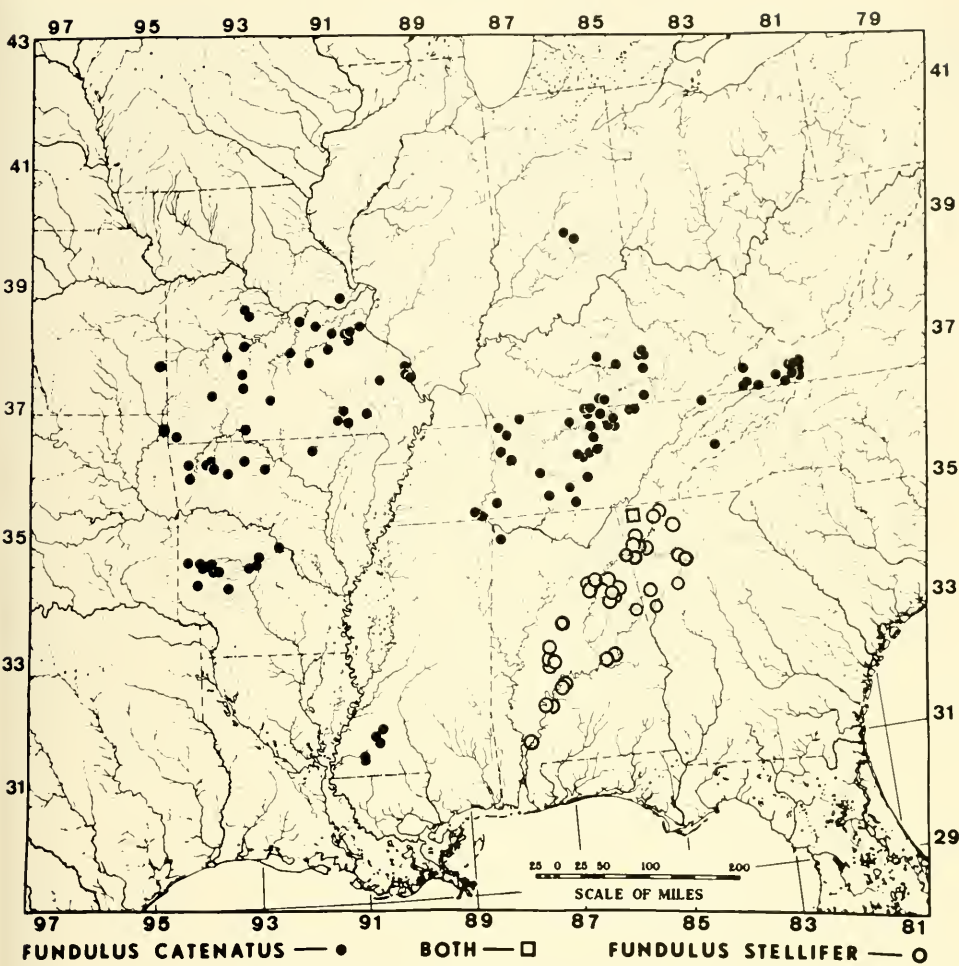


Figure 2. Distribution of studfish collections listed in Material Examined and peripheral localities in Kansas and Oklahoma.

have not been described several times, confused, or misidentified as has so often happened to members of the genus *Fundulus*. Even though the two forms show considerable overlap in meristic and morphometric characters, consistent differences in pigmentation, male breeding colors, and pharyngeal dentition lead me to regard *F. catenatus* and *F. stellifer* as valid allopatric species.

KEY TO THE STUDFISHES

Eight to ten continuous rows of lateral dots centered on each scale; dots brown or olive in females and juveniles, orange to orange-red in nuptial males; scale outlines

not sharp, particularly in males; males without black margin on dorsal fin but some males with black subterminal caudal band; pharyngeal teeth of large individuals at most peg-like; nuptial males usually without contact organs on dorsal fin or caudal peduncle; lateral scale rows usually 12-14. In streams ultimately tributary to the Mississippi River
Fundulus catenatus.

Dots randomly distributed or at most in six to nine irregular rows on upper sides, dots not centered on each scale, size of dots irregular; dots brown or olive in females and juveniles, orange to dark red in nuptial males; scale outlines sharp, particularly in

females and juveniles; some males with black margins on both dorsal and caudal fins; some pharyngeal teeth in large individuals molariform; males often with contact organs on dorsal fin and caudal peduncle; lateral scale rows usually 14-16. In streams ultimately tributary to the Alabama or Chattahoochee Rivers *Fundulus stellifer*.

RANGE

Distribution of Material Examined and Peripheral Records (Figure 2) gives a good representation of the range of the studfishes. A few of the apparent distributional gaps are not real but reflect that no material from those areas was studied.

Fundulus catenatus

Moore (1968, p. 112) gave the range of *Fundulus catenatus* as:

"Upland tributaries of the Tennessee, Cumberland, and Green Rivers in Kentucky, Tennessee, Virginia, and Alabama: clear streams of the Ozark region in Kansas, Missouri, Oklahoma, and Arkansas; Red River tributaries in southwestern Arkansas; the Homochitto River in Mississippi; and the upper part of the East Fork of White River, Indiana."

Previous records of *F. catenatus* in Kansas are probably not valid (Cross, 1967, pp. 230-231), however, Bass and Triplett (1967) have taken a single specimen from Drywood Cr., Crawford County Kansas, a stream ultimately tributary to the Little Osage River. The populations cited in this paper represent geographical areas from which samples seemed to me to be reasonable homogeneous and statistically distinct from those of adjacent areas.

The "Ozarks Population" inhabits the small creeks draining into the Mississippi River on the Missouri (western) side of the river from just north of the confluence of the Missouri and Mississippi Rivers south to Cape Girardeau Co., Missouri. Smith (1965) included *F. catenatus* as a hypothetical addition to the fish fauna of Illinois because of its occurrence in these small tributaries in adjacent Missouri counties. The populations north of the Missouri River in the Big Creek system seem to have crossed the river from the south and established

themselves in historical times (W. L. Pflieger, in litt., 1966). It thus seems possible that pioneers from the Ozarks population in Missouri may someday cross the Mississippi River into Illinois. The specimens included in the Ozarks population are generally distributed throughout the Missouri Ozarks and south into central Arkansas where samples from tributaries to the Arkansas River were referred to this population. I have not examined material from the Neosho R. in NE Oklahoma (Branson, 1967).

The "Ouachita Population" includes samples from the Ouachita River drainage in Arkansas and one sample from the Saline River of southwestern Arkansas, a tributary of the Red River.

The "Homochitto River Population" is confined to the Homochitto River system in the southwestern corner of Mississippi.

The "Tennessee River Population" includes samples from the Tennessee and Duck Rivers and their tributaries in Tennessee, Alabama, and Georgia. CU 50009 (22 specimens) from Powell River, Claiborne Co., Tenn., just south of the western tip of Virginia (see Figure 2) clearly belongs with the Tennessee River population and not with the Virginia population.

The "Virginia Population" includes samples from the Clinch River and the North Fork of the Holston River in Virginia. Although several of the collections I examined had locality data simply as "Holston River, Va." or just as "Va.," I assume that they came from the North Fork of the Holston River or the Clinch River. Ross and Carico (1963) listed 25 localities for *F. catenatus* from the North Fork drainage and none for the Middle Fork or South Fork of the Holston River.

The "Cumberland River Population" includes samples from the Cumberland River and its tributaries in Tennessee and Kentucky. The "Green River Population" includes samples from Green River drainage in Kentucky and Tennessee. The "Indiana Population" is a relict population in tributaries to the East Fork of the White River in Indiana (see Gerking, 1945, p. 22; Map 69, p. 78).

Fundulus stellifer

Fundulus stellifer occurs in Alabama River tributaries in Alabama, Georgia and Polk

Co., Tennessee, but is not known from the Tombigee River which joins the Alabama River from the west just north of Mobile Bay. It also occurs in several of the upper tributaries of the Chattahoochee River in northern Georgia (Figure 2). There is a problematic record of one specimen from West Fork Chickamauga Creek, a Tennessee River tributary in northeastern Georgia (see Material Examined). This record is of considerable interest because it is from the range of *F. catenatus* and an *F. catenatus* was present in the collection. I believe this is a valid record of *F. stellifer* syntopic with *F. catenatus* rather than the result of mixing of specimens from two different localities or some similar mistake. However, intensive collecting of this locality 17 September 1967 netted a single juvenile *F. catenatus*. All other easily accessible sites in the small drainage were visited also; two offered no studfish habitat, one seemed suitable but no studfish were present and *F. catenatus* only was present at two other sites. One party of fishermen was present at the syntopic locality when we arrived at 0900 and another party came before 1030. Perhaps the record of *F. stellifer* at this locality indicates bait release rather than a natural population, but it seems doubtful that fishermen would transport bait from the sparsely populated Alabama River tributaries of the area when bait fishes are so abundant in the Tennessee River tributaries.

The "Upper Coosa River Population" includes samples from northern Georgia, except for those from Chattahoochee tributaries. Included were samples from Walker, Murray, Whitfield, Cobb, Gordon and Pickens Cos. The "Middle Coosa River Population" comprises all samples from the Coosa River and its tributaries in Alabama and in Chattooga and Cherokee Cos., Ga.

The "Alabama River Population" included samples from the Alabama River proper and its small tributaries. The "Cahaba River Population" and the "Tallapoosa River Populations" included samples from tributaries to those streams respectively in Alabama and Georgia. The "Chattahoochee River Population" includes all samples from the Chattahoochee system.

METHODS

All rays of the dorsal, anal and left pectoral fins were counted at their bases. Caudal ray number is total branched caudal rays plus 2 and counts were made only on large individuals since the number of branched rays increases with ontogeny. Lateral scales were counted as described by Hubbs and Lagler (1947). Lateral scale rows were counted on the left side only in a zig-zag fashion from and including the scale on the dorsal midline at the anterior of the dorsal fin base ventrally to the last scale before the ventral midline.

Standard Length measurements were made to the nearest mm for the fish discussed in the section on contact organs. All other measurements, including Standard Length, were made with Helios mm dial calipers to three figures. Standard Length (SL), Predorsal Length (PDL), Caudal Peduncle Depth (CPD), Pelvic Fin Length (P2L), Depressed Dorsal Fin Length (DL), Depressed Anal Fin Length (AL), and Anal Fin Base Length (AB) were taken as described by Hubbs and Lagler (1947). Body Depth (BD) and Head Width (HW) were taken as described by Thomerson (1966). Head Length (HL) was taken from the rear of the bony operculum at the dorsal terminus of the gill slit to the tip of the snout. Head Depth (HD) was taken at the level of the posterior margin of the preopercle.

Color descriptions were made from 35 mm color slides of live and preserved specimens, from field notes and from live specimens kept in aquaria. All adult males in the collections listed under Material Examined were examined with a dissecting microscope and sketches were made showing distribution of contact organs. Notes on pigmentation were also made for these males.

VARIATION IN MERISTIC CHARACTERS

Meristic data are presented in tabular form (Tables 1-6). Populations are not considered to have significant differences for a given count unless the sum of 2 standard errors (2SE) of one plus 2SE of the other is less than the difference between the two means. This interpretation and that of Figures 5 and 6 presenting morphometric data follow Hubbs and Hubbs (1953).

TABLE 1. Number of dorsal rays in *Fundulus catenatus* and *Fundulus stellifer*.

POPULATION	12	13	14	15	16	17	N	Average	SD	2SE
<i>Fundulus catenatus</i>										
Ozarks			14	188	58	9	269	15.2	.58	.07
Ouachita	1	5	64	29	1		100	14.2	.60	.12
Homochitto R.		10	71	19			100	14.1	.53	.11
Tennessee R.		13	65	48	2		128	14.3	.54	.09
Virginia		18	38	9			65	13.9	.63	.16
Cumberland R.		3	29	56	12		100	15.2	.81	.16
Green R.		3	45	62	7		117	14.6	.64	.12
Indiana				3	3		6			
<i>Fundulus stellifer</i>										
Upper Coosa R.		6	30	19	3		58	14.3	.74	.19
Middle Coosa R.		43	76	6	1		126	13.7	.58	.10
Alabama R.	1	27	44	1			73	13.6	.54	.12
Cahaba R.		33	55	1			89	13.6	.50	.10
Tallapoosa R.	1	7	1				9	13.0		
Chattahoochee R.		5	14	11	1		31	14.3	.77	.28

Fundulus catenatus

Observed range of variation in dorsal ray number is 12 to 17 (Table 1). Specimens from the Ozarks and Cumberland River populations tend to have relatively high dorsal ray numbers (avg. 15.2 for both) and these populations are significantly different from all other populations of *F. catenatus* in this character. The two populations with lowest average number of dorsal rays are the Homochitto River (14.1) and Virginia (13.9) populations. The Homochitto River population is not separable from either the Ouachita

or Tennessee River populations with this character; however, the Virginia and Tennessee River populations can be separated.

Anal ray number (Table 2) varies from 13 to 18. The highest averages are again those of the Ozarks and Cumberland River populations (avg. 16.2 for both), but the Green River Population also tends toward high counts (avg. 16.1). The Homochitto River, Ouachitas, and Virginia populations tend toward low counts (avgs. 14.9, 15.2, and 15.3 respectively). Distribution of anal ray counts tends to parallel distribution of

TABLE 2. Number of anal rays in *Fundulus catenatus* and *Fundulus stellifer*.

POPULATION	13	14	15	16	17	18	N	Average	SD	2SE
<i>Fundulus catenatus</i>										
Ozarks			12	138	48	6	204	16.2	.60	.08
Ouachita	2	10	53	33	2		100	15.2	.72	.14
Homochitto R.	1	13	78	8			100	14.9	.50	.10
Tennessee R.		2	47	68	19		136	15.8	.70	.12
Virginia		2	39	22	1		64	15.3	.57	.14
Cumberland R.			14	59	24	3	100	16.2	.68	.14
Green R.			12	69	19		100	16.1	.55	.11
Indiana				2	4		6			
<i>Fundulus stellifer</i>										
Upper Coosa R.	1	15	34	9			59	14.9	.69	.18
Middle Coosa R.	3	58	59	5	1		126	14.5	.65	.12
Alabama R.	1	31	37	3			72	14.5	.61	.14
Cahaba R.	2	56	30				88	14.3	.52	.11
Tallapoosa R.		4	5				9	14.6		
Chattahoochee R.	1	8	21	1			31	14.7	.59	.21

TABLE 3. Number of left pectoral rays in *Fundulus catenatus* and *Fundulus stellifer*.

POPULATION	14	15	16	17	18	19	N	Average	SD	2SE
<i>Fundulus catenatus</i>										
Ozarks			38	131	31		200	17.0	.58	.08
Ouachita			25	67	8		100	16.8	.55	.11
Homochitto R.		1	4	21	63	11	100	17.8	.72	.14
Tennessee R.	1	4	41	66	9	1	122	16.7	.73	.13
Virginia		11	44	8			63	16.0	.55	.14
Cumberland R.	1	1	34	61	3		100	16.6	.61	.12
Green R.		7	48	39	6		100	16.4	.71	.14
Indiana				4	2		6			
<i>Fundulus stellifer</i>										
Upper Coosa R.		1	11	38	8		58	16.9	.63	.17
Middle Coosa R.		4	49	60	12	1	126	16.7	.74	.13
Alabama R.			33	39	1		73	16.6	.57	.13
Cahaba R.		8	60	22			90	16.2	.56	.12
Tallapoosa R.		1	1	4	3		9	17.0		
Chattahoochee R.		1	13	17			31	16.5	.57	.20

dorsal ray counts; most specimens have one more anal than dorsal ray but some have the same number, one less, or two more.

Number of left pectoral rays (Table 3) varies from 14 to 19. The Virginia sample average (16.0) is significantly the lowest and the average (17.8) for the Homochitto River sample is significantly the highest. Coefficient of Difference between these two populations is 1.38, slightly above the conventional criterion for subspecific differentiation (Mayr, Linsley, and Usinger, 1953, p. 146). However, Coefficients of Difference between the Homochitto population and the Ozarks, Ouachita, or Tennessee

River populations are all less than 1.0. The same is true of Coefficients of Difference between the Virginia population and the Tennessee River, Cumberland River, or Green River populations.

Caudal Ray number (Table 4) varies from 15 to 18. All populations tend to have subequal proportions of individuals with 16 or 17 caudal rays. The lowest average number of caudal rays is 16.2 (Green River) and the highest is 16.7 (Homochitto River). There is thus a weak trend from higher number of caudal rays in the south to lower number of caudal rays in the north.

Observed range of lateral scale row num-

TABLE 4. Number of caudal rays in *Fundulus catenatus* and *Fundulus stellifer*.

POPULATION	14	15	16	17	18	N	Average	SD	2SE
<i>Fundulus catenatus</i>									
Ozarks		2	57	24	3	86	16.3	.58	.13
Ouachita		3	17	18	3	41	16.5	.74	.23
Homochitto R.			18	22	4	44	16.7	.63	.20
Tennessee R.		1	19	24	2	46	16.6	.61	.18
Virginia			11	7		18	16.4	.25	.12
Cumberland R.		3	20	27	1	51	16.5	.64	.18
Green R.		6	31	13	2	52	16.2	.69	.19
Indiana			6			6			
<i>Fundulus stellifer</i>									
Upper Coosa R.		1	11	17		29	16.6	.57	.21
Middle Coosa R.			5	26	27	58	16.4	.64	.17
Alabama R.	1		36	17		54	16.3	.56	.15
Cahaba R.	1	17	33	1		52	15.7	.58	.16
Tallapoosa R.			6	3		9	16.3		
Chattahoochee R.		5	14	4		23	16.0	.64	.27

OZARKS							
5	OUACH.						
5	3	HOMO- CHITTO					
4	2	3	TENN. R.				
5	4	4	3	VA.			
3	3	4	4	4	CUMB. R.		
4	4	5	5	4	1	GREEN R.	
4.3	3.5	4.0	3.5	4.0	3.2	3.8	$\bar{X}$

Figure 3. Matrix giving the number (out of 6) of meristic characters in which the various populations of *Fundulus catenatus* differ significantly. $\bar{X}$ is the arithmetic average number of significantly different characters for each population. Population labels apply to the horizontal row to the left of the label and the vertical column below the label.

ber (Table 5) is 11 to 16. Average number of lateral scale rows ranges from 13.2 (Ouachita, Green River) to 14.4 (Virginia). The Virginia sample average differs significantly from the Tennessee River average (13.7).

Number of lateral scales is given in Table 6. In the aquarium studfish fight and individuals may be almost completely scaled.

Though such intensive fighting may be an artifact caused by crowding in the aquarium, many studfish collected in the wild show patches of regenerated scales. These individuals were not counted unless the original number of scales was obvious. However, there is also considerable irregularity of scale rows that does not involve regenerated scales. When I felt that the lateral scale count was questionable, I counted the lateral scales on the right side and discarded the counts if there was more than 1 scale difference. Thus, even though the count is often difficult to make, the wide range of variation (38–52) seems real. The average (42.4) for the Homochitto River Population is significantly the lowest. Other populations with low average number of lateral scales are the Ozarks (avg. 43.5) and Ouachita (avg. 44.5) populations. These southern and western populations thus contrast with the eastern populations which have averages ranging from 45.3 to 46.4. These differences are, however, far below the level required to justify recognition of subspecies.

Figure 3 is a matrix showing the number of meristic characters (out of six) in which the various populations of *F. catenatus* differ. The average number given for each population is the arithmetic mean and is an unweighted estimate of the amount of divergence of each population from all other *F. catenatus* populations. The Ozarks population is most divergent and the Cumberland River population the least divergent.

TABLE 5. Number of lateral scale rows in *Fundulus catenatus* and *Fundulus stellifer*.

POPULATION	11	12	13	14	15	16	17	18	N	Average	SD	2SE
<i>Fundulus catenatus</i>												
Ozarks		6	70	112	12				200	13.6	.68	.10
Ouachita		20	46	31	3				100	13.2	.78	.16
Homochitto R.	1	22	29	37	10	1			100	13.4	1.00	.20
Tennessee R.		6	35	67	13	1			122	13.7	.74	.13
Virginia			8	24	23	5			60	14.4	.99	.26
Cumberland R.	2	12	42	37	7				100	13.3	.85	.17
Green R.		15	48	37					100	13.2	.69	.14
Indiana			2	4					6			
<i>Fundulus stellifer</i>												
Upper Coosa R.			1	11	21	13	2		48	15.1	.87	.25
Middle Coosa R.			3	27	36	35	17	1	119	15.4	1.09	.20
Alabama R.				12	46	12	3		73	15.1	.70	.16
Cahaba R.				5	42	26	14		87	15.6	.83	.18
Tallapoosa R.					6	2	1		9	15.4		
Chattahoochee R.			1	7	15	6	2		31	15.0	.91	.33

TABLE 6. Number of lateral scales in *Fundulus catenatus* and *Fundulus stellifer*.

POPULATION	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	N	Average	SD	2SE
<i>Fundulus catenatus</i>																			
Ozarks		5	13	18	35	33	30	27	15	13	8		1	1		199	43.5	2.29	.33
Onachita			1	8	11	13	16	24	12	10	1	3	1			100	44.5	2.04	.40
Honochitto R.	3	6	12	5	27	17	12	12	6							100	42.4	2.01	.40
Tennessee R.		2	2	6	9	12	16	14	25	13	11	4	5	2	1	122	45.3	2.60	.47
Virginia				3	1	8	3	10	13	7	8	4	2	1		60	45.7	2.34	.60
Cumberland R.				2	5	6	14	10	11	18	15	8	6	2	3	100	46.4	2.56	.51
Green R.	1			5	7	12	13	11	14	16	14	2	3	2		100	45.4	2.46	.49
Indiana					2				3	1						6			
<i>Fundulus stellifer</i>																			
Upper Coosa R.		1	2	5	4	6	5	6	5	5	5		4	1		49	44.7	3.01	.86
Middle Coosa R.		2	1	4	5	10	14	19	21	18	17	9	6	3		129	45.9	2.51	.44
Alabama R.	1	3	3	9	12	12	13	7	4	6	2	1				73	43.3	2.36	.55
Cahaba R.	3	3	7	15	12	17	12	8	6	3	2					88	42.7	2.27	.49
Tallapoosa R.							1	2		1		1	3		1	9	42.2		
Chattahoochee R.					1	6	5	6	7	6						31	44.9	1.52	.55

U					
COOSA					
2	M				
	COOSA				
2	1	ALA.			
		R.			
6	2	3	CAHABA		
2	2	2	4	CHAT'E	
3.0	1.8	2.0	3.8	2.5	$\bar{X}$

Figure 4. Matrix giving the number (out of 6) of meristic characters in which the various populations of *Fundulus stellifer* differ significantly. Interpretation as for Figure 3.

Fundulus stellifer

Fundulus stellifer populations from the Alabama River-Coosa River system show a trend toward high average number of rays in all fins (pelvic not counted) upstream and low average number of rays downstream. The Cahaba River sample tends to have the lowest average numbers of fin rays.

Number of dorsal rays (Table 1) varies from 12 to 16 and all populations have a modal number of 14. However, means (14.3) for the Upper Coosa River and Chattahoochee River samples are significantly higher than means for the other populations. Number of left pectoral rays (Table 3) varies from 15 to 19 and the Cahaba River average (16.2) is significantly lower than averages for other Alabama drainage populations. Caudal ray number (Table 4) varies from 14 to 17. With the exception of the Cahaba River and the Chattahoochee River samples, individuals with 16 or 17 caudal rays occur in all populations in subequal proportions. These samples have unusually high percentages of individuals with 15 caudal rays and the Cahaba River average (15.7) is significantly the lowest for the Alabama drainage samples.

Trends in distribution of average numbers of scales do not parallel distribution of fin ray averages. Left lateral scale row number

varies from 13 to 18 (Table 5). The Cahaba River sample has the highest average number (15.6) and the Chattahoochee River sample the lowest (15.0). The remarks above regarding the causes of extreme variation in lateral scale number of *F. catenatus* also apply to *F. stellifer*. Observed range of variation in lateral scale number (Table 6) is 38 to 52. The Cahaba and Tallapoosa River samples have the lowest average number of lateral scales (42.7, 42.2) and the Middle Coosa River sample the highest (avg. 45.9).

Figure 4 is a matrix for *F. stellifer* drawn in the same fashion as Figure 3. The Cahaba River sample has the highest average number of significantly different meristic characters and the Middle Coosa River sample the lowest.

Comparison of *Fundulus catenatus* and *Fundulus stellifer*

Dorsal Rays—*Fundulus stellifer* tends to have fewer dorsal rays than *F. catenatus* but there is almost complete overlap in observed range of variation (none with 17 rays for *F. stellifer*, 9 from the Ozarks sample for *F. catenatus*). The Middle Coosa River, Alabama River, Cahaba River and Tallapoosa River samples of *F. stellifer* have lower average numbers of dorsal rays than any *F. catenatus* sample (Table 1), but the Upper Coosa River and Chattahoochee River samples have higher average numbers than three of the *F. catenatus* samples and are identical to the Tennessee River sample (avg. 14.3) in this parameter.

Anal Rays—The Homochitto River *F. catenatus* sample is not separable from the Upper Coosa River and Chattahoochee River *F. stellifer* samples of this character. The other three large samples of *F. stellifer* had lower averages than all *F. catenatus* and the other six large *F. catenatus* samples had higher averages than all *F. stellifer* samples.

Left Pectoral Rays—Range of variation in average number of left pectoral rays (16.0 to 17.8) for the *F. catenatus* samples includes the range of variation (16.2 to 16.9) seen in *F. stellifer* samples.

Caudal Rays—Only the Cahaba River *F. stellifer* sample average (15.7) is significantly outside the range of variation in this parameter for *F. catenatus* samples (16.2 to 16.7).

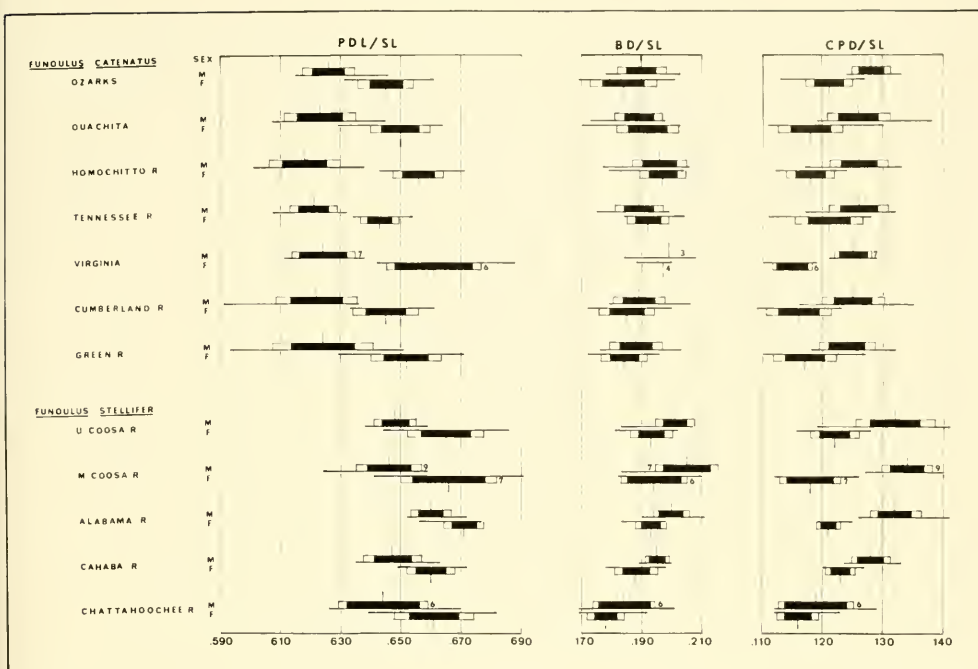


Figure 5. Geographic variation in morphometric characters in *Fundulus catenatus* and *Fundulus stellifer*. Samples are 10 individuals except where number is given. PDL-Predorsal Length, BD-Body Depth, CPD-Caudal Peduncle Depth, SL-Standard Length. Drawn following Hubbs and Hubbs (1953).

Lateral Scale Rows—There is considerable overlap in range of variation in this character (*F. catenatus*, 11 to 16; *F. stellifer*, 13 to 18), but it is the most divergent of the meristic characters studied. The highest average for an *F. catenatus* sample (14.4, Virginia Population) is significantly lower than the lowest *F. stellifer* average (15.0, Chattahoochee River Population).

Lateral Scales—The range of average number of lateral scales for *F. catenatus* samples (42.4 to 46.4) includes the range of variation (42.7 to 45.9) for *F. stellifer* samples.

MORPHOMETRIC CHARACTERS

There is considerable variation in body proportions in both species of studfish. Several characters also exhibit marked sexual dimorphism. In addition to the characters shown in Figures 5, 6, and 7, other proportional measurements involving characters mentioned above in the section on Material and Methods were made but showed only random variation and are not presented.

There is striking sexual dimorphism in Predorsal Length (Figure 5) in *F. catenatus* and to a lesser extent in *F. stellifer*. Even though the body outline of males and females is different (Figure 1) there is no sexual dimorphism of Body Depth in either species but males do tend to have deeper caudal peduncles than females. This character is fairly consistent from population to population in *F. catenatus*, but there is considerable variation in *F. stellifer*. Male *F. stellifer* from the Coosa River and Alabama River populations tend to have deeper caudal peduncles than most *F. catenatus* males. The Cahaba River population resembles *F. catenatus* in this character and the Chattahoochee River population appears most slender.

Head Length (Figure 6) varies considerably within populations but there does not seem to be a consistent pattern of either sexual or geographic variation in *F. catenatus* except that Tennessee River females have significantly shorter heads than males. The Alabama River *F. stellifer* also show signifi-

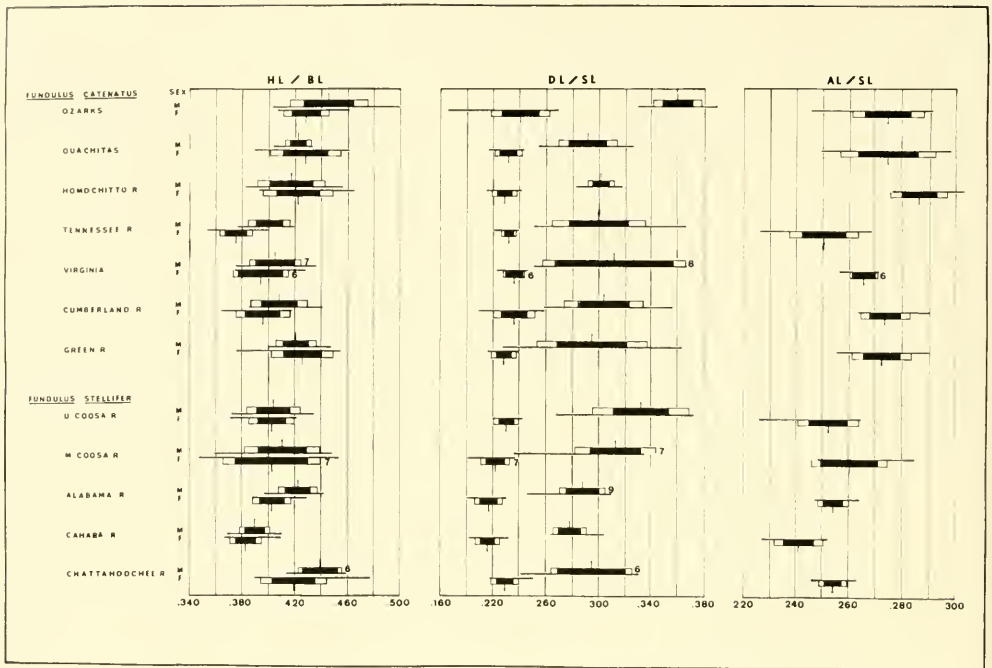


Figure 6. Geographic variation in morphometric characters in *Fundulus catenatus* and *Fundulus stellifer*. Samples are 10 individuals except where number is given. HL-Head Length, BL-Body Length, DL-Depressed Dorsal Fin Length, AL-Depressed Anal Fin Length, SL-Standard Length. Drawn following Hubbs and Hubbs (1953).

cant sexual dimorphism in this character and difference between the Alabama and Cahaba River populations is significant when males are compared with males and females with females. There is also a significant difference between Cahaba and Chattahoochee River populations.

Dorsal Fin Length (Figure 6) shows a high degree of sexual dimorphism with little overlap between the sexes in either species. With the exception of Ozarks population *F. catenatus*, there is little variation in female dorsal fin length. Part of the variation seen in the males is seasonal. Nuptial males have slightly elongated dorsal fins.

Male studfish have dorsal and anal fins of approximately the same length but anal fin length averages 17% greater than dorsal fin length in female *F. catenatus* and 13% greater in female *F. stellifer*. The anal fin of the female digs into the substrate during spawning and her anal rays are stouter than the dorsal rays. In female studfish longer anal fins tend to be elongate and pointed but

shorter anal fins tend to be rectangular. The Tennessee River females have significantly shorter anal fins than those of other *F. catenatus* populations. The Homochitto River females have significantly longer anal fins than females from other eastern populations of *F. catenatus*. The means for *F. stellifer* samples, except the Middle Coosa River sample, are significantly lower than those of *F. catenatus* samples except for the Tennessee River population. None of the *F. stellifer* samples can be separated from the Tennessee River *F. catenatus* sample using this character. The Cahaba River sample mean is significantly lower than the other *F. stellifer* sample means except for the Upper Coosa River sample mean.

Both species show sexual dimorphism in Pelvic Fin Length. The observed range of P2L/SL for *F. catenatus* females is 0.102 to 0.136, for *F. stellifer* females 0.106 to 0.131, average for both 0.115. This average ratio is compared with the distribution of P2L/SL for males in Figure 7. Large males and

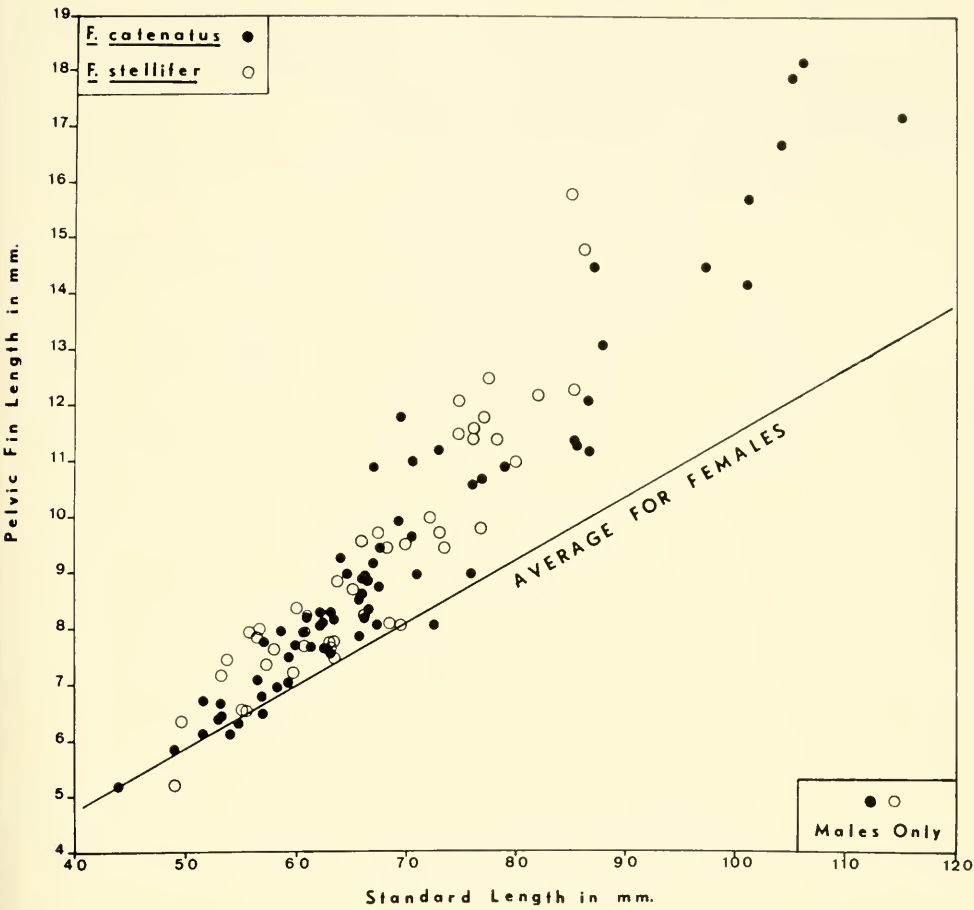


Figure 7. Relationship between Pelvic Fin Length and Standard Length in *Fundulus catenatus* and *Fundulus stellifer*. Pooled data from all populations, including largest males from each.

smaller males in breeding condition tend to have proportionately longer pelvic fins in both species.

MALE CONTACT ORGANS AND BREEDING COLORS

During the breeding season, males of *F. catenatus* and *F. stellifer* develop contact organs (Newman, 1907, 1909). These are particularly noticeable on the anal fin rays, and the presence of contact organs on the anal fin of *F. stellifer* was noted by Fowler (1916, Pl. 1). The distribution of contact organs is similar in the two studfishes (Figure 8), but usually *F. catenatus* males are less "prickly" than *F. stellifer* males, and contact

organs on the sides of the body are confined to an area between the bases of the dorsal and anal fins. Figure 8A shows the distribution of contact organs usually seen on breeding *F. catenatus* males, but there are often no contact organs on the dorsal or pectoral fins in this species. In both species a few anal fin contact organs may be present in males taken at any time of year. As the fish come into breeding condition, the anal fin organs are proliferated and contact organs on the cheeks and opercles develop concurrently or soon after. Development of the lateral contact organs begins at midbody between the bases of the dorsal and anal fins and in general proceeds further anterior and posterior

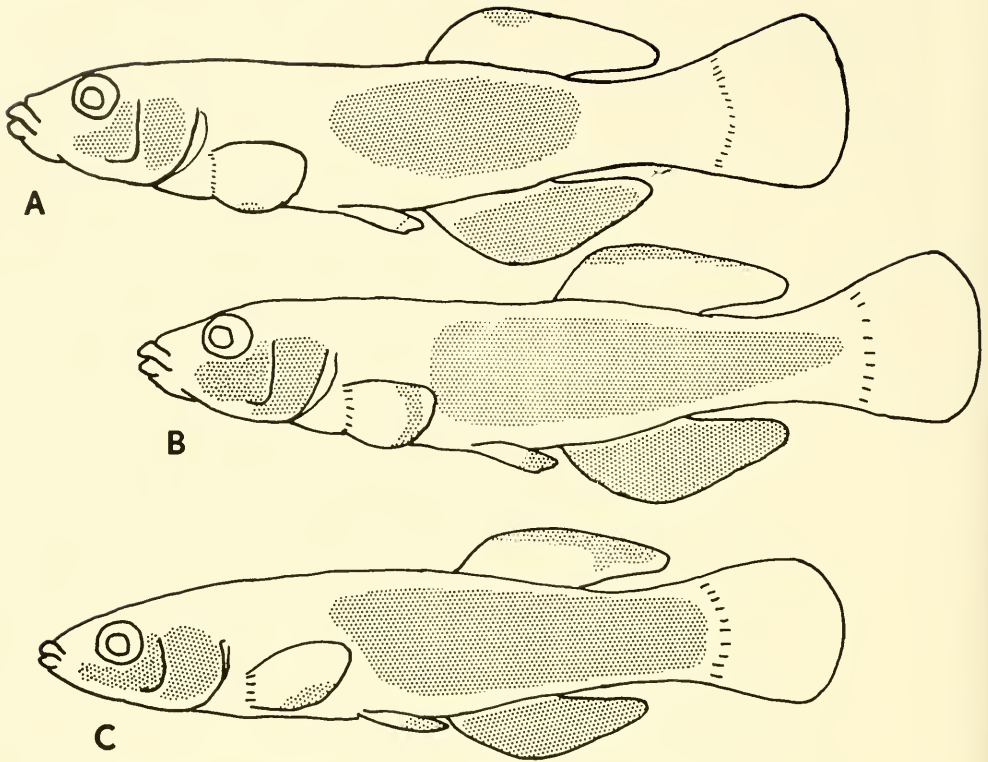


Figure 8. Sketches of studfish males; dotted area represents extent of development of contact organs. A. Usual extent of contact organs in *Fundulus catenatus*. B. Unusually extensive development of contact organs in *Fundulus catenatus*. C. Usual extent of contact organs in *Fundulus stellifer*.

in *F. stellifer* than in *F. catenatus* (Figure 8A and C). I have seen only two specimens of *F. catenatus* with contact organs on the lateral scales of the caudal peduncle; one of these is sketched in Figure 8B. Development of contact organs on the pelvic rays, on both sides of the fin, is seen in most high males but presence of contact organs on the pectoral fins is less common. About half the breeding males of both species have a few organs on the anteroventral surface of the pectoral fin. Occasional males have one or two contact organs on the posterodorsal surface of the pectoral fin. Less than half the *F. catenatus* males examined had contact organs on the dorsal fin, and these were generally confined to the anterior half of the fin. Almost all *F. stellifer* males had dorsal fin contact organs with the greatest concentration in the posterior half of the fin. 1

examined a number of breeding female studfish and found no contact organs.

Female studfish do not show seasonal color changes. The patterns shown in Figure 1B and D are seen in live specimens in varying shades and intensities of brown. Nonbreeding males resemble the females in drab coloration and pattern, but nuptial males are spectacularly colored.

Fundulus catenatus males occur in two color forms. As given in Table 7, various percentages of males exhibit a subterminal black band in the caudal fin. This band intensifies during the breeding season but is discernable in all months of the year. Placement and sharpness of the band are variable. Some males, particularly those from the Cumberland and Green rivers, have a wide (about 2 mm) yellow to orange band distal to the black band. In others, particularly those from the Ouachita and Ozarks popu-

TABLE 7. Occurrence of males with black caudal fin band in *Fundulus catenatus* and *Fundulus stellifer*.

POPULATION	Number	Percent with Band
<i>Fundulus catenatus</i>		
Ozarks	109	44
Ouachita	12	42
Homochitto	60	0
Tennessee	30	20
Virginia	14	36
Cumberland	30	43
Green	34	12
<i>Fundulus stellifer</i>		
All	142	58

lations, the yellow to orange band may be quite narrow. In two of the Ouachita specimens, the black band is essentially terminal, as it is in *F. stellifer*. The margins of the band, particularly the distal margin, are usually sharp, but in some males it is a black zone rather than a sharply defined band. The band is represented by disconnected blotches of black pigment in many males from the Ozarks population.

Only one of the males examined showed any concentrated black pigments at the margin of the dorsal fin (CU 49857, Cumberland River population). His black dorsal pigment resembles that of an *F. stellifer* male with less than maximum expression of this character. Dorsal fin coloration in breeding *F. catenatus* males varies from dark slate blue overall, which appears blue in the water, to yellow distally and translucent yellow-grey proximally, which looks yellow in the water. When the dorsal fin is dark there is sometimes a narrow yellow or orange margin but I have never seen the white or cream margin of the dorsal and caudal fin described by Garman (1895). The interradial membranes of the dorsal and the proximal halves of the anal, caudal, and sometimes the pelvic and pectoral fins are marked with elliptical orange spots. These are largest and most intense in the dorsal fin. The anal fin is transparent yellow-grey proximally and bright translucent yellow distally. The color pattern of the pectoral and pelvic fins is similar but not so intense. The caudal fin is greyish and translucent in transmitted light but blue in

reflected light. Males without the black subterminal band exhibit the yellow to orange terminal band on the caudal fin.

The head pattern is similar to that of *F. stellifer*. There is a very conspicuous light blue or blue-green iridescent patch from the upper anterior quarter of the orbit to the corner of the gape. The iris is bright yellow-green to dark with a silver reflecting margin around the pupil. In some specimens there is an area of dark pigment directly ventral to the preocular light patch. The cheeks and opercular area are marked with a random pattern of circular orange spots. Those on the operculum are about twice the diameter of the others on head and body. The lower half of the head and the gular and branchiostegal regions are yellow, but the upper lateral surfaces of the head are livid yellow-green. The dorsum and top of the head are olive grading into either sky blue or green laterally. The color of the sides depends on the angle and quality of the light striking them. There may be an area of disordered orange spots just behind the head or all the spots may be linearly arranged, one spot per scale, from the gill openings to the bases of the caudal rays. The spots are slightly separated but give the impression of 10 to 12 continuous orange lines down the sides. Viewed in the water in sunlight against a dark background, a male in high color gives the impression of a fish with a solid red-orange body.

Fundulus stellifer males also occur in two color forms. A black margin on the dorsal and caudal fins may be either present or absent. Data from all populations are pooled in Table 7, but males of both kinds were present in all populations where reasonable size samples were available. A few males with black borders on the dorsal and caudal fins also had less distinct black borders on the pectoral and pelvic fins.

Body color in males is a livid sky blue, grading into white on the belly and bluish-brown on the dorsum. The fins are clear yellow, and there are rows of elliptical orange spots in the interradial membranes of the dorsal fin and in the basal halves of the caudal and anal fins. There may also be a few such spots near the base of the pectoral fins. If the caudal fin border is absent the caudal fin may be slate grey rather than yellow.

low. There is a brilliant iridescent pre-ocular patch as in *F. catenatus*, but it is yellow-green rather than bluish. The iris is also yellow-green, and there is a light blue-green, diffuse iridescent patch on the gill cover behind the eye. The orange spots on the head are irregular in size and arrangement like those of *F. catenatus* and the body pattern is similar to the head pattern. Dark orange spots are concentrated on the dorsolateral region of the body with only a few scattered on the lower sides. The spots on the caudal peduncle are linearly arranged but not so consistently as those of *F. catenatus*.

OTHER CHARACTERS

Male studfish average larger than females in most collections; however, the largest *F. catenatus* I have seen was a 118 mm SL female from the Ozark population. Dr. David A. Etnier kindly informed me of an unusually large 98 mm SL male *F. stellifer* from the Conasauga River in Polk Co., Tennessee. The largest males in the collections listed under Material Examined were 86 or 87 mm SL. With the exception of the Homochitto population, a large *F. catenatus* male is over 100 mm SL. The Homochitto population seems dwarfed and the largest specimen (of 768) from there was an asexual individual 76 mm SL.

Fundulus catenatus has regular rows of spots on the sides of the body. These dots are red or red-orange in breeding males but an alcoholic male specimen appears plain because of leaching of pigment by the preservative. The pattern in *F. stellifer* is similar but with fewer spots not necessarily on the centers of the exposed scale fields nor arranged in the orderly manner seen in *F. catenatus*. The few Tallapoosa River specimens seem more *F. catenatus*-like than specimens from other *F. stellifer* populations in the arrangement of their lateral spots. In addition to the difference in arrangement of the lateral dots there is a consistent difference in the pigmentation of the scale borders. As seen in Figure 1, *F. stellifer* has a regular cross-hatched appearance in contrast to the more uniform background pattern of *F. catenatus*. The cross-hatching extends to the base of the anal fin in *F. stellifer* and stops a few scales short in *F. catenatus*. The differences in development of scale border pigmentations al-

low identification of juveniles, although they are more similar than are the adults (Figure 9). I have not seen enough very small specimens of the two species to point out differences between them at sizes below approximately 14 mm SL.

The intestinal contents of *F. stellifer* seem finely ground in comparison to those of *F. catenatus*, probably as a result of chewing with the stout pharyngeal molars (Figure 10). The pharyngeal bones of *F. stellifer* are massive compared to those of similar size *F. catenatus* and molars are developed both on the inferior pharyngeal bones and on the pharyngobranchials. The corresponding teeth in *F. catenatus* are pegs with hooked tips. They resemble the hooked blade-like teeth of other species of *Fundulus*, for example *F. notatus*, but are stronger with an expanded circular cross section. Snails form an important item of diet for *F. stellifer* (J. D. Satterfield, personal communication) and I have seen snail shells in the feces of *F. catenatus*. One might guess from its comparatively more massive pharyngeal bones and dentition that of the two, *F. stellifer* eats more mollusks.

DISCUSSION

Fundulus catenatus is an aggressive and adaptable small-stream fish widely distributed in the upland areas of the Mississippi Valley. It probably originated in the eastern uplands where I have recognized four distinct populations in roughly a third of the range. The distribution of *F. catenatus* crosses a number of zoogeographic barriers. Particularly striking is the uniformity of the Ozarks population over an area approximately equal to the eastern uplands. Many Ozarkian fishes have been sufficiently isolated in the White River system and the Missouri Ozark streams tributary to the Missouri and Mississippi Rivers to diverge even to the species level (Gilbert, 1964, pp. 104-5), but *F. catenatus* samples from the two areas are not significantly different.

The broadly-ranging Ozark population is the most divergent in terms of meristic characters studied (Figure 3). It seems closest to the Cumberland River population, than to the Tennessee and Green River populations. Not only does relative morphological uniformity over such a large area suggest

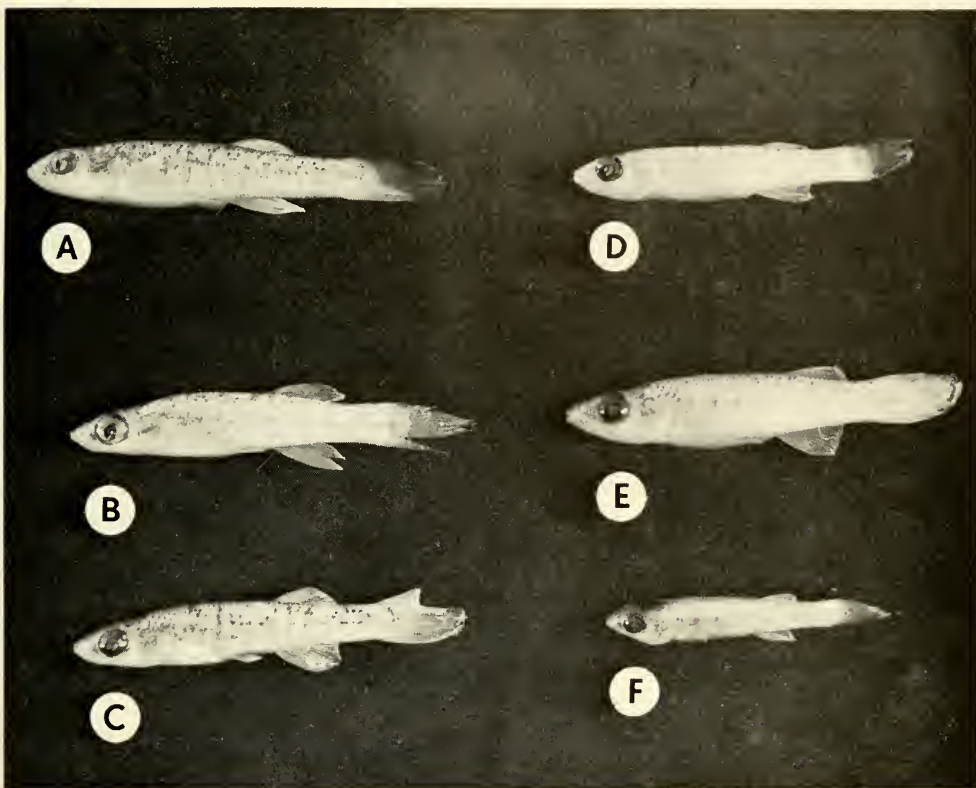


Figure 9. Juvenile studfish—*Fundulus catenatus*: A. TU 15132 (SL 24.6 mm), B. KU 6661 (SL 24.1 mm), C. KU 11550 (SL 24.2 mm). *Fundulus stellifer*: All from JDS, D. SL 22.1 mm, E. SL 25.4 mm, F. SL 17.2 mm.

that the Ozarks population is of recent origin compared to the populations in the eastern uplands, but there is evidence that Ozarkian *F. catenatus* are still rapidly moving into suitable habitats around the margins of the Ozarks. As mentioned above, *F. catenatus* seems to have crossed the Missouri River and become established in the Big Creek system in recent historical time. The recent Neosho River records may be from a population established naturally from the White River (Branson, 1967) or from bait releases (Hall, 1956). In any case, *F. catenatus* is common there now. It seems significant that *F. catenatus* is absent from the Flint Hills region of Kansas, even though several other species with Ozarkian affinities occur there (Cross, 1967). Probably *F. catenatus* was not present in the Ozarks when access to the Flint Hills was possible.

The Ouachita population shows surprising

divergence from the Ozarks population, is most like the Tennessee River population and is not particularly divergent from the other eastern populations. It thus seems probable that the Ozarks and Ouachita populations originated from separate invasions of the Interior Highlands by fish from the eastern populations.

The widely disjunct Homochitto population does not show as much divergence in meristic characters as the Ozarks population but seems unique in the absence of black-banded males and the small maximum adult size. Conditions in the Homochitto drainage are considerably different from those in the Interior Highlands or eastern uplands and the characters mentioned above could have strong adaptive significance. The small size of the Homochitto fish may be correlated with reduced food supply. In any case, the numbers taken in the collections I have ex-

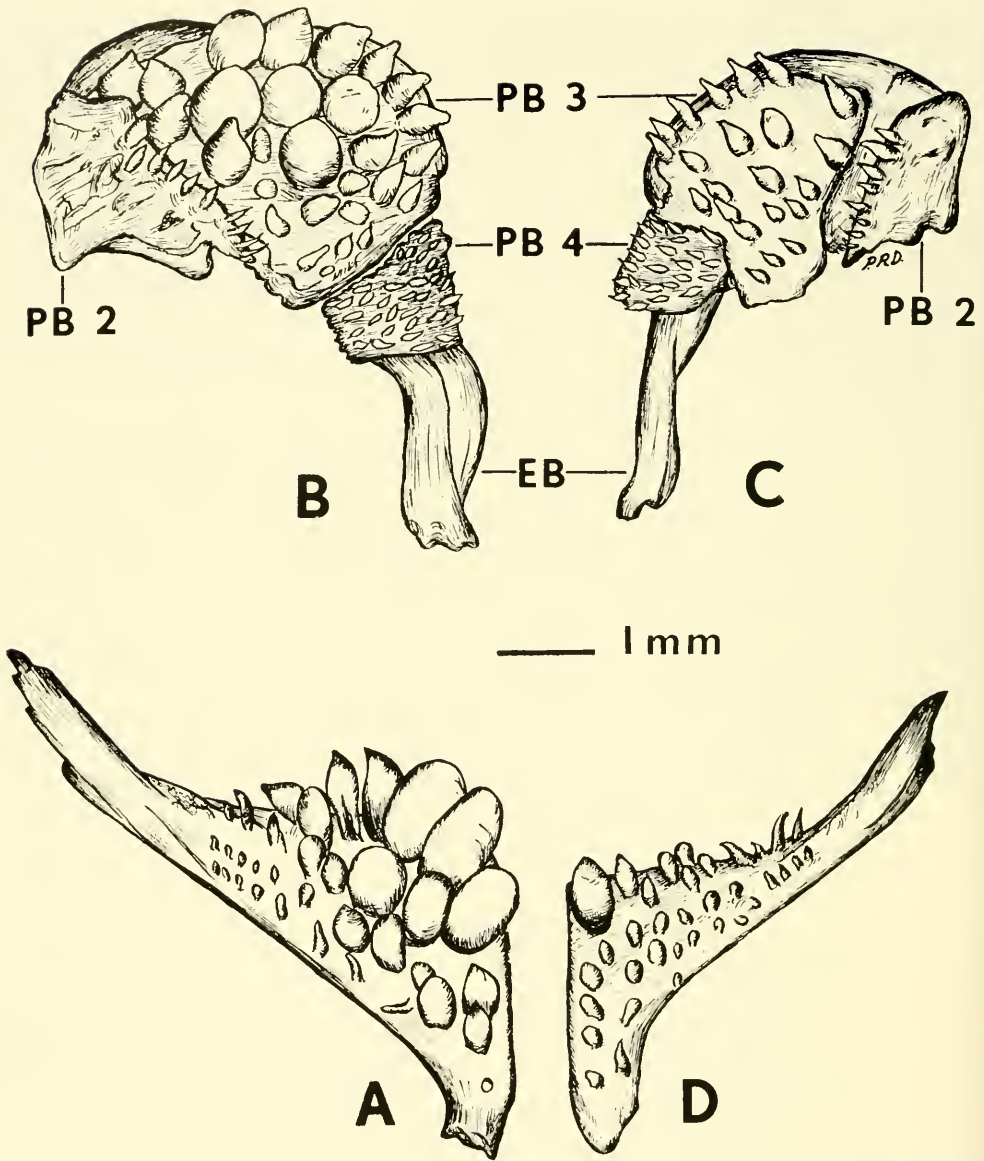


Figure 10. Pharyngeal arches of studfish; A. and B. from a 71.4 mm SL *Fundulus stellifer* (TU 35029), C. and D. from a 70.0 mm SL *Fundulus catenatus* (SIUE, JET 66-10). A. Right lower arch, dorsal view, anterior down. B. Right upper arch, ventral view, anterior to the upper left. C. Left upper arch, ventral view, anterior to upper right. D. Left lower arch, dorsal view, anterior down.

amined indicate that *F. catenatus* is successful in maintaining relatively dense populations in the Homochitto River system. The small fish and southern location of this population suggest a similarity to *F. stellifer*, but their pharyngeal teeth, lateral scale row count

and pigment patterns show no such similarity. Perhaps gene flow with other populations of *F. catenatus* is maintained even though there is a broad expanse of unsuitable habitat separating the Homochitto River from the *F. catenatus* populations in the cen-

tral highlands. The Homochitto fish may represent a postglacially isolated relict of a population distributed through the Lower Mississippi Valley during glacial periods when lowered sea level caused rejuvenation of small tributaries of the Lower Mississippi River. Alternatively the population could have been established by individuals tributary-hopping during interglacial periods when the Mississippi River was cooler, clearer and swifter flowing than it is today. If this were the case, the Homochitto population might have received immigrant individuals from both eastern and western populations.

The major observed differences between *F. catenatus* and *F. stellifer* are: general pigmentation, distribution of contact organs, male breeding colors and pharyngeal dentition. *Fundulus stellifer* could be duplicated by relatively slight changes in an *F. catenatus* stock and indeed a few *F. catenatus* individuals, as noted above, show tendencies toward the *F. stellifer* condition. Pharyngeal dentition is very similar in small individuals of the two species. Greenwood (1964) found differences of approximately the same magnitude between the pharyngeal bones and associated structures of wild individuals and an aquarium-raised specimen of the snail-eating cichlid *Astatoreochromis alluaudi*. The aquarium-raised specimen had an adequate diet but did not receive snails until late in life. Its pharyngeal teeth and bones were less massive (Figure 3, p. 5, Greenwood, 1964) than those of any of the wild individuals. The differences between the pharyngeal teeth and bones of larger *F. catenatus* and *F. stellifer* (Figure 10) may thus be correlated with difference in food habits rather than with difference at the genetic level. Whatever their cause, differences between the two species seem to be consistent.

The ancestors of *F. stellifer* were probably a stock much like present day *F. catenatus* which became isolated in the Alabama River system. Whether this was the result of a major faunal exchange between the Tennessee and Alabama systems or the result of local stream capture is not clear, but the latter seems more likely. If *F. catenatus* had entered the Alabama system in large numbers, stabilizing selection acting on the somewhat generalized and flexible *F. catenatus*

gene pool would probably have produced just another population of *F. catenatus*, one perhaps resembling the Homochitto population.

If the ancestor of *F. stellifer* was a *F. catenatus*-like fish, the more massive pharyngeal dentition of *F. stellifer* is thus probably a result of further specialization for snail eating. It is my impression that, even though the faunas of the Alabama and Chattahoochee systems are rich in fish species, the density of small fishes in streams inhabited by *F. catenatus* is much higher than in streams inhabited by *F. stellifer*. The varieties and kinds of habitats seem to be similar in the two areas, so perhaps the greater number of individual fishes in *F. catenatus* habitat is correlated with availability of food organisms. If *F. stellifer* lives in a less rich habitat, further specialization of snail eating would be of adaptive value by increasing utilization of a food supply little used by other small stream fishes. The evolution of *F. stellifer* may have been relatively rapid and recent because the characters separating it from *F. catenatus* seem of obvious adaptive significance but characters of less obvious adaptive significance show little divergence.

MATERIAL EXAMINED

Collections are listed by population, state, county and museum number. Collections deposited Illinois Natural History Survey (INHS) and Southern Illinois University, Edwardsville (SIUE) are not given catalog numbers. Complete data are given for the syntopic collection. Other museum abbreviations are used as follows: The Academy of Natural Sciences of Philadelphia, ANSP; Auburn University, AU; University of Alabama Ichthyological Collection, UAIC; Cornell University, CU; Indiana University, IU; University of Kansas, Museum of Natural History, KU; University of Michigan, Museum of Zoology, UMMZ; Smithsonian Institution, USNM; personal collection of James D. Satterfield, JDS; Tulane University, TU; University of Richmond, UR. Number of specimens in each collection is given in parentheses. All specimens were examined and counts were made on 885 *F. catenatus* and 386 *F. stellifer* from the collections listed below. Distribution of these collections is shown in Figure 2.

Allopatric *Fundulus catenatus*

Ozarks.—Missouri: Lincoln Co.; SIUE (14), SIUE (44)—Franklin Co.; INHS (7)—Carter Co.; UMMZ 104684 (25)—Wright Co.; INHS (3)—Osage Co.; INHS (6)—Phelps Co.; INHS (25)—Morgan Co.; KU 6501 (11)—Camden Co.; UMMZ 150336 (14)—Dallas Co.; KU 7837 (19)—Hickory Co.; KU 7811 (6)—Crawford Co.; UMMZ 148448 (9)—Dent Co.; INHS (9), INHS (7), KU 7614 (11)—Wayne Co.; UMMZ 117246 (12)—Cape Girardeau Co.; INHS (8), INHS (2), INHS (25)—Madison Co.; INHS (6)—Shannon Co.; KU 7652 (10), KU 7674 (2), UMMZ 102491 (38)—Dade Co.; KU 5503 (50)—Green Co.; KU 7856 (19)—Taney Co.; KU 10926 (112)—McDonald Co.; CU 42324 (6). Arkansas: Sharp Co.; UMMZ 116378 (40)—Marion Co.; KU 8012 (53), KU 9864 (31)—Boone Co.; UMMZ 123522 (88), KU 6661 (8)—Newton Co.; UMMZ 175430 (6)—Madison Co.; UMMZ 123892 (43), UMMZ 123425 (54), UMMZ 123859 (27)—Washington Co.; UMMZ 127769 (7), CU 36506 (2).

Onachita.—Arkansas: Pulaski Co.; INHS (2)—Saline Co.; CU 42245 (17)—Garland Co.; TU 14250 (3)—Montgomery Co.; KU 6166 (25), KU 6143 (7)—Pike Co.; KU 6133 (48). UMMZ 81112 (8), KU 6135 (11)—Howard Co.; KU 6115 (5)—Polk Co.; KU 6907 (10), UMMZ 81110 (2).

Homochitto River.—Mississippi: Amite Co.; UMMZ 144728 (2), UMMZ 155340 (12), TU 7447 (18)—Franklin Co.; TU 11991 (12), TU 16623 (142), TU 19766 (57), TU 19851 (32), TU 15132 (141), TU 23952 (78), UMMZ 161204 (4), TU 7208 (176)—Lincoln Co.; TU 32916 (32), TU 28895 (60)—Copolah Co.; UMMZ 154371 (2).

Tennessee River.—Tennessee: Sevier Co.; KU 8935 (1)—Coffee Co.; TU 30299 (61)—Bedford Co.; UMMZ 121529 (1)—Lincoln Co.; TU 30289 (7)—Marshall Co.; KU 10684 (12)—Marshall and Maurv Cos.; UMMZ 121477 (44)—Lewis Co.; UMMZ 105213 (28)—Wayne Co.; UMMZ 177703 (4)—Humphreys Co.; UMMZ 168314 (33)—McNairy Co.; TU 10593 (2). Tennessee: Claiborne Co.; CU 56009 (22). Alabama: Franklin Co.; UMMZ 177723 (6).

Virginia.—Virginia: ? Co. (Holston R.), ANSP 7304-35 (32)—Smyth Co.; UR 1979 (1), UR 899 (2), UR 940 (1), USNM 40368 (3), UMMZ 96899 (11), USNM 102428 (1)—Washington Co.; UMMZ 130779 (1), UMMZ 130808 (4), UMMZ 130788 (3)—Scott Co.; CU 50078 (1), ANSP 74207 (4), ANSP 74235 (1)—Lee Co.; USNM 104043 (1).

Cumberland River.—Kentucky: Pulaski Co.; CU 50059 (26)—Wayne Co.; CU 50090 (8)—Cumberland Co.; CU 50042 (3), KU 11554 (1). INHS (2). Tennessee: Fentress Co.; KU 11532 (14), CU 50191 (6)—Overtown Co.; UMMZ 125196 (2)—Clay Co.; UMMZ 125228 (3), UMMZ 125258 (13), UMMZ 125341 (3)—Jackson Co.; KU 11550 (24), CU 50028 (9)—

Smith Co.; CU 49857 (19)—Putnam Co.; KU 8947 (1)—Warren Co.; UMMZ 175257 (5)—Cannon Co.; KU 11678 (10)—Sumner Co.; UMMZ 96323 (26)—Wilson Co.; KU 11588 (15)—Rutherford Co.; KU 11482 (7)—Montgomery Co.; INHS (1)—Houston Co.; INHS (8).

Green River.—Kentucky: Lincoln Co.; KU 5722 (17), KU 7253 (41)—Casey Co.; UMMZ 178028 (17)—Taylor Co.; KU 11620 (26)—Allen Co.; KU 11641 (4), INHS (20), INHS (13). Tennessee: Macon Co.; UMMZ 165377 (42), TU 14532 (25).

Indiana.—Indiana: Shelby Co.; IU 397 (5)—Johnson Co.; INHS (2).

Syntopic Collection

Tennessee River.—Georgia: Walker Co.; W Fork Chickamauga Cr. 1.3 mi. W jct. Hwy. 143 and Hwy. 341 on Hwy. 143, 23 June 1964, R. D. Suttks and Env. Biol. Class, TU 34975 (1 ♂ *F. stellifer*, 1 ♀ *F. catenatus*).

Allopatric *Fundulus stellifer*

Upper Coosa River.—Georgia: Pickens Co.; TU 38346 (9), TU 40732 (9)—Murray Co.; TU 7334 (4), TU 27974 (5), TU 37542 (27)—Gordon Co.; TU 35029 (85)—Walker Co.; TU 27575 (1)—Whitfield Co.; USNM 200704 (4).

Middle Coosa River.—Georgia: Chattooga Co.; TU 34978 (2), TU 33367 (3)—Floyd Co.; USNM 31070 (8), USNM 101159 (1), JDS (2), JDS (140). Alabama: Cherokee Co.; JDS (73)—Etowah Co.; USNM 43475 (3)—Calhoun Co.; TU 40782 (2), UAIC 636 (6), USNM 63136 (4), USNM 200705 (6)—St. Clair Co.; UAIC 648 (6), UAIC 657 (4)—Talladega Co.; UAIC 639 (5), UAIC 880 (1), UAIC 890 (2).

Alabama River.—Alabama: Dallas Co.; TU 35357 (39), TU 32640 (28)—Wilcox Co.; TU 40325 (1), TU 2971 (1), TU 3058 (5)—Clark Co.; TU 35344 (1).

Cahaba River.—Alabama: Shelby Co.; USNM 43504 (8)—Bibb Co.; UAIC 2035 (1)—Perry Co.; TU 29899 (18), TU 30095 (15), TU 37703 (11), UAIC 962 (49).

Tallapoosa River.—Georgia: Carroll Co.; UAIC 1312 (1). Alabama: Randolph Co.; UAIC 1379 (2)—Elmore Co.; TU 15280 (3), UAIC 1279 (3).

Chattahoochee River.—Georgia: Fulton Co.; CU 28249 (2), TU 12167 (1), TU 26125 (1), AU 718 (24)—Heard Co.; AU 512 (3).

ACKNOWLEDGMENTS

I wish to express my appreciation to curators who loaned specimens from their collections: Dr. James E. Böhlke, ANSP; Dr. John S. Ramsey, AU; Dr. H. T. Boschung, UAIC; Dr. Edward C. Raney, CU; Dr. Joseph S. Nelson, IU; Dr. Ernest A. Lachner, USNM; and Dr. W. S. Woolcott, UR. The following persons also extended every courtesy during

visits to their institutions; Dr. Philip W. Smith, INHS; Dr. Frank B. Cross, KU; Dr. Robert R. Miller, UMMZ; and Dr. Royal D. Suttkus, TU.

Drs. Reeve M. Bailey, W. L. Burger, David A. Etnier, Neal Foster, Mr. Robert E. Jenkins, Dr. George A. Moore, Mr. William L. Pflieger, Dr. John S. Ramsey, Mr. William Smith-Vaniz, and Mr. James D. Williams all aided the study by supplying color notes, locality data or other useful information. Mr. William L. Pflieger also read the manuscript and offered many helpful comments. Mr. James D. Satterfield kindly supplied considerable information from his study of *Fundulus stellifer* and allowed me to examine specimens from his personal collection. A number of SIUE students and former students, particularly Mrs. Norma Brown, Leland Hill, Dennis Trotter, Steven L. Smith and Gerald L. Smith, helped with various aspects of the study. Ronald Twillman, Gary D. Waller and Drs. Robert J. and Joyce Goldstein helped make the collections from W Fork Chickamauga Cr. in Georgia. We thank the Goldsteins for their hospitality during this collecting trip.

Figure 10 was drawn by Pamela R. Drake. The University Photographic Service assisted in preparing the Figures. Dr. Leonard C. Jones wrote a program and showed me how to operate the GE 265 time sharing computer facility at SIUE to treat the data presented in Figures 5 and 6. The study was supported by a Faculty Research Grant from the Graduate School, Southern Illinois University.

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SWINGLEUS POLYCLITHROIDES GEN. ET SP. N.
(MONOGENEA: GYRODACTYLIDAE) FROM
FUNDULUS GRANDIS BAIRD AND GIRARD¹

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ABSTRACT

Swingleus polyclithroides, a new genus and species of gyroductylid Monogenea, is described from the gulf killifish, *Fundulus grandis* Baird and Girard. This species is unique in the possession of the following combination of characters, 1) marginal hooks distributed in two groups as in *Polyclithrum mugilini* Rogers, 1967, 2) a peduncular bar as in *Gyrodactylus megacanthus* Wellborn and Rogers, 1967, *G. trematoelithrus* Rogers, 1967, and *G. prolongis* Hargis, 1955, 3) absence of a deep (dorsal) bar, and 4) the presence of lateral accessory bars. The presence of a peduncular bar indicates a strong relationship to the species of *Gyrodactylus* possessing this structure while the marginal hooks being distributed in two groups and the presence of lateral accessory bars shows a relationship to *Polyclithrum* Rogers, 1967. Since the above mentioned features are intermediate between the subfamilies Gyrodactylinae and Polyclithrinae, the subfamily status of *Swingleus* is unclear at this time.

The species described herein was collected as part of a survey of fish parasites being conducted by the Southeastern Cooperative Fish Parasite and Disease Project. Hosts were collected with a seine. The fish were immediately placed in a container of 1:4,000 formalin solution (Putz and Hoffman, 1963). After 1 hour, formalin was added to the container to make a 5% solution. The parasites were later recovered for study in the laboratory from the solution. Specimens were treated and measured as described by Rogers and Wellborn (1965). All measurements are in microns. Averages of measurements

are given followed by the range in parentheses. Drawings were made with a camera lucida. The keys to the members of Gyrodactylidae in Yamaguti (1963) were used to determine the status of the present species.

Swingleus gen. n.

Generic diagnosis: Gyrodactylidae: head bilobed, head organs present. Pharynx pyramidal, gut bifurcate, not confluent posteriorly. Cirrus with spine and several spinules. Testis not observed with certainty, appears preovarian. Peduncular bar present. Haptor with one pair of anchors, ventral bar, pair of lateral winglike bars, and 16 marginal hooks. Dorsal bar absent. Anchor base with cap of dense tissue. Marginal hooks distributed in two groups, each of first three pairs located on anterolateral margin, remaining five pairs on posterior margin. Parasitic on fish.

Type species: *Swingleus polyclithroides* sp. n.

Type host: *Fundulus grandis* Baird and Girard.

Type locality: Mobile Bay at Mobile Causeway, Baldwin County, Alabama.

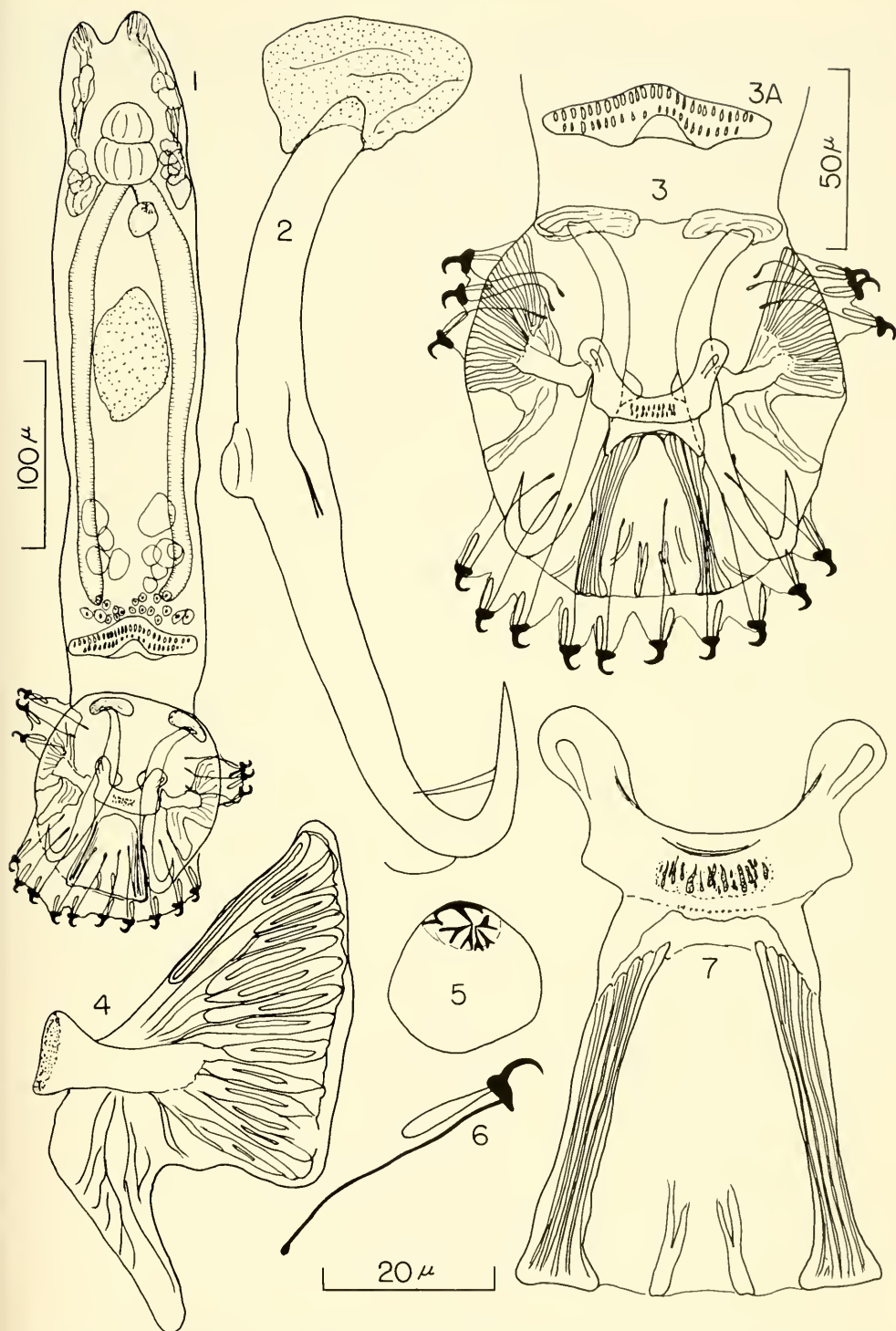
Remarks: This genus appears to be closely related to *Polyclithrum* Rogers, 1967 (Rogers, 1967a) by possessing lateral bars and having hooks distributed in two groups. Anchor shape, ventral bar shape, and the presence of a peduncular bar indicate a strong relationship to certain species of *Gyrodactylus* occurring on *Fundulus* spp., (see Wellborn and Rogers, 1967; Rogers, 1967b). *Gyrodactylus prolongis* Hargis, 1955, was collected at the same time as *S. polyclithroides* and anchor and ventral bar shape

¹ Supported by the Southeastern Cooperative Fish Parasite and Disease Project. (In part by Sport Fish Restoration funds.)

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Figures 1-7. *Swingleus polyclithroides* gen. et sp. n. Scale of 100 microns applies to Fig. 1; 50 micron scale applies to Fig. 3, 3A; and 20 micron scale applies to all other figures. 1. Entire worm, ventral view. 2. Anchor. 3. Haptor. 3A. Peduncular bar. 4. Lateral winglike bar. 5. Cirrus. 6. Hook. 7. Ventral bar and shield.

of these two species are very similar. A peduncular bar occurs on *G. prolongis* similar to the peduncular bar of *S. polyclithroides*. This bar has a series of small ridges and depressions appearing as spines. Hargis (1955) reported this bar as an "anteriorly directed skirt whose edge is armed by several cuticularized points." The similarities to the above mentioned species of *Gyrodactylus* (subfamily Gyrodactylinae) and to *Polyclithrum mugilini* (subfamily Polyclithrinae) makes the subfamily status of *S. polyclithroides* unclear at this time. This genus is named in honor of Dr. H. S. Swingle of Auburn University.

Swingleus polyclithroides sp. n.
(Figures 1-7)

Host and locality: *Fundulus grandis* Baird and Girard, Gulf killifish, Mobile Bay at Mobile Causeway, Baldwin Co., Alabama.

Location on host: Fins and body.

Specimens studied and measured: Ten.

Type specimens: Holotype and 2 paratypes, USNM Helm. Coll. Nos. 70445 and 70446; paratypes in author's collection.

Description: Length 479 (390 to 620), width 94 (80 to 130). Cephalic area with two prominent lobes, each containing several spines. Cephalic glands prominent, lateral to posterior edge of pharynx; head organs well developed. Pharynx bilobed in side view, posterodorsal lobe larger, 35 (30 to 39) in diameter, anteroventral lobe 28 (25 to 39) in diameter. Gut bifurcate with crura ending blindly at level of gonads. Cirrus (Fig. 5) located ventrally to left of and posterior to pharynx, with large spine and 2 to 5 spinelets, diameter 15 (13 to 19). Testis preovarian? Ovary with many diffuse eggs in various stages of development. Peduncular bar present, with many small oblong to elongate depressions (Fig. 3A), greatest length of bar 66 (63 to 69); width 19 (18 to 20). Haptor (Fig. 3) circular to oblong, with one pair of anchors supported by a ventral bar and lateral "winglike" bars, and 16 marginal hooks. Haptor length 109 (105 to 135), width 96 (70 to 108). Anchors (Fig. 2) with prominent knobs apparently representing vestigial dorsal bar, points with arc membranes (Mizelle and Kritsky, 1967) and

small membranes arising from shaft near point similar to "wings" of dactylogyrids, base of anchor shaft with dense cap of tissue; anchor length 96 (92 to 100), width 10 (9 to 11), point length 23 (21 to 25). Ventral bar (Fig. 7) articulated in prominent folds on anchor shaft, with shield terminating at posterior edge of haptor, anterolateral projections of ventral bar with thickened area, central portion of bar with coarse striations. Bar 37 (33 to 45) by 11 (9 to 12), anterolateral projection length 12 (10 to 13). Shield of ventral bar with coarse striations on margins and 2 forked ridges posteromedially, shield length 46 (42 to 48), width 42 (40 to 45). Lateral bars (Fig. 4) winglike, with coarse striations distally, base articulated to anchor shaft, length along bar axis 37 (34 to 39). Marginal hooks 16 in number, located dorsally on haptor, first 3 pairs in 2 groups at anterolateral edge of haptor, remaining 5 pairs on posterior edge of haptor (Figs. 1, 3). Shaft of each hook (Fig. 6) with slight enlargement proximally, shaft length 32 (30 to 33), hook length 7 to 8, lamella length 12 (11 to 13).

Remarks: This is the only species reported in the genus. It was found on the host in association with *Gyrodactylus prolongis* Hargis, 1955. The name *polyclithroides* refers to the similarity to the genus *Polyclithrum*.

ACKNOWLEDGMENTS

Thanks are extended to Mr. John R. Kelley, who initially collected this species, and to Messrs. Shih-Ming Chien, S. K. Johnson, and M. V. Rawson for subsequent collections. Dr. John S. Ramsey confirmed host identifications.

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December 16, 1969

A NEW TREMATODE, *LEPIDODIDYMOCYSTIS*
IRWINI N. G., N. SP. (DIDYMOZOIDAE) FROM
A MARINE FISH, *MENTICIRRHUS NASUS*

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ABSTRACT

A new didymozoid belonging to Didymozoinae Ishii, 1935, is described. It is named after its collector, Mr. Roy Irwin, a graduate student at Tulane University. It was found underneath the scales below the lateral line of a marine teleost, *Menticirrhus nasus* (Gunther, 1868), from N. Mazatlan. The generic name refers to this special habitat. The most outstanding features of this trematode include: (1) flat semicircular hindbody with a distinct longitudinal furrow on concave side, (2) acetabulum present, (3) common genital pore opening at truncate apex of prominent genital papilla, (4) long esophagus, (5) single undivided ovary and single undivided vitelline gland, (6) cylindrical sinuous egg reservoir, (7) metratrem ciliated throughout its length, and (8) eggs not embryonated when laid.

INTRODUCTION

Twenty specimens on which the present report is based were taken by Mr. Roy Irwin, a graduate student at Tulane University, together with scales from below the lateral line of *Menticirrhus nasus* collected in N. Mazatlan, Mexico.

They had been previously fixed in formalin *in situ*; they were isolated from the cysts attached underneath the scales, refixed in 10% formalin, and stained with Delafield's hematoxylin. We gratefully acknowledge Mr. Irwin's furnishing the material for our examination. The worms, enclosed in pairs in transparent circular cysts, were so strongly flattened underneath the scales that the whole mounts clearly revealed the internal anatomy, making sectioning unnecessary. This parasite represents an undescribed didy-

mozoid for which *Lepidodidyimoecystis irwini* n. g., n. sp. is proposed.

DESCRIPTION

Based on 20 whole mounts. Cysts flattened circular, about 3-5 mm in diameter. Forebody flattened claviform, conspicuously papillated at head end, finely annulated for remaining part, 0.53-0.82 mm long with maximum width of 0.13-0.32 mm posterior to its middle, whence it tapers gradually forward to a more or less sharp point, attached to anterior end of hindbody on its concave side. Hindbody flattened, semicircular, truncate anteriorly and rather pointed posteriorly, 3.6-5.1 $\times$ 2.44-3.58 mm; forebody embedded in a distinct longitudinal furrow on concave side of hindbody. Oral sucker terminal, oblong, 66-82 $\times$ 43-52 μ , weakly muscular, directly followed by spherical muscular pharynx 42-49 μ in diameter. Immediately behind pharynx clustered large claviform pharyngeal gland cells, with attenuated ends converging toward posterior end of pharynx. Esophagus narrow, 0.46-0.87 mm long, provided with a coat of small glandular cells throughout its length, bifurcating immediately as it enters hindbody; ceca lined with epithelia, strongly winding throughout length of hindbody and terminating at its posterior end. A cup-shaped, weakly muscular acetabulum 59-91 μ in diameter lies on concave side of hindbody near base of forebody. Testes paired, long, tubular, winding, usually close to each other, rarely divergently in anterior part of hindbody near concave side; in type they reach just beyond equatorial level, with their

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ends somewhat swollen. Vas deferens narrow throughout its length, without forming a definite seminal vesicle, distinctly ciliated just before uniting with metraterm at base of genital papilla. Genital papilla projecting prominently ventral to oral sucker, 25-40 μ in diameter, flattened at apex where wide common genital pore opens. Ovary a single, long, narrow tubule, 23-53 μ wide, irregularly winding in axial region of hindbody, reaching to near its posterior end. Vitelline gland also a single, irregularly winding, narrow tubule, 30-67 μ wide, extending on convex side of hindbody to its extreme posterior end, its anterior portion turns back on itself at truncate anterior end of hindbody and after describing several turns joins proximal end of ovary. This end is often swollen like proximal end of vitelline gland; seminal receptacle 74-178 $\times$ 45-97 μ , situated at this genital junction. Uterine duct provided with a thick coat of gland cells, runs sinuously forward to recurrent portion of vitelline gland, where it passes to uterus proper, the latter winding backward to posterior end of the hindbody and then forward to anterior end of hindbody and once more backward, to lead into egg reservoir near the posterior extremity, thus forming four loops altogether and occupying greater part of hindbody; egg reservoir cylindrical, sinuous, close to concave side of hindbody; metraterm well differentiated in forebody, distinctly ciliated inside throughout its length. Egg oval, thick-shelled, operculate, 12-15 $\times$ 9-11 μ , ova contained in metraterm not yet embryonated, almost all in 2-cell stage. Excretory system not made out.

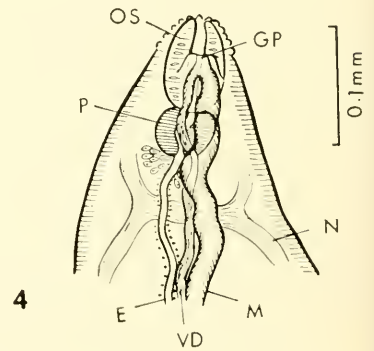
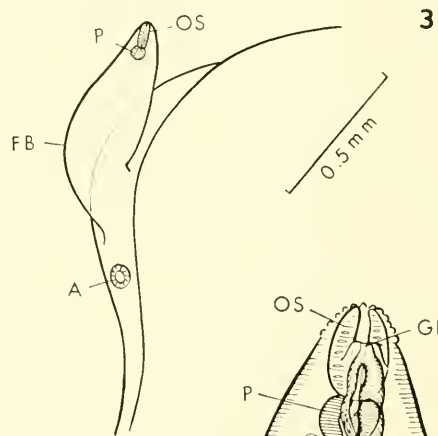
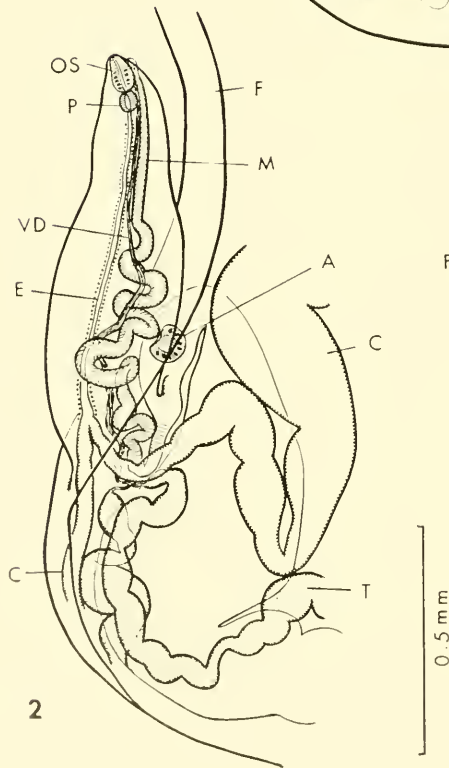
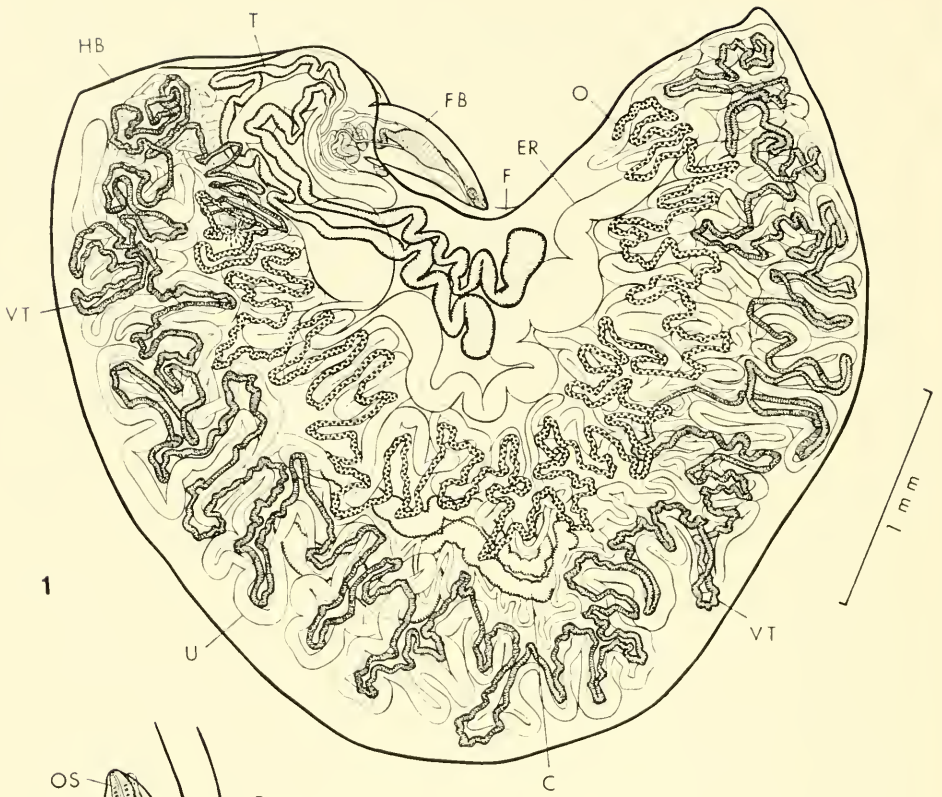
DISCUSSION

In general internal anatomy and habitat this genus bears a marked resemblance to *Dermatodidymocystis* Yamaguti (especially *D. viviparoides* Yamaguti) (in press) but differs from it in the possession of: (1) a longitudinal furrow and an acetabulum on the concave side of the hindbody, (2) a prominent genital papilla ventral to the oral sucker, (3) a uterus regularly forming four longitudinal loops before leading into a prominent egg reservoir, and (4) unembryonated eggs, an important character since most other didymozoid eggs are generally embryonated *in utero*. There is no doubt

that the genus in question belongs in the Didymozoinae. It is named in reference to the special habitat (beneath the scales), and defined as follows:

GENERIC DIAGNOSIS. Didymozoidae, Didymozoinae. Complete hermaphrodites, encysted in pairs. Forebody small, flattened claviform, attenuated anteriorly, attached to hindbody near its anterior end, papillated at head end, and finely annulated elsewhere. Hindbody smooth, approximately semicircular, truncate at anterior end, conical at posterior end, with distinct longitudinal furrow on concave side, where a cup-shaped, weakly muscular acetabulum is present near base of forebody. Oral sucker terminal, weakly muscular; pharynx spherical, muscular, with well developed postpharyngeal gland cells behind. Esophagus long, narrow, surrounded by small glandular cells throughout its length, bifurcating as it enters hindbody. Ceca strongly winding, terminating at posterior extremity of hindbody. Testes two, tubular, winding in anterior half of hindbody close to concave side; vas deferens narrow, not forming definite seminal vesicle, ciliated just before uniting with metraterm. Common genital pore opening at apex of prominent truncate genital papilla ventral to oral sucker. Ovary single, tubular, long, undivided, winding in axial region of hindbody and reaching to near its posterior end. Vitelline gland tubular, long, undivided, winding from extreme posterior end of hindbody to its anterior end, where it turns backward to join anterior end of ovary, so that genital junction lies near truncate anterior end of hindbody. Seminal receptacle present. Uterus occupying all available space of hindbody, forming four longitudinal loops before leading into conspicuous egg reservoir which extends longitudinally along concave side of hindbody; metraterm well differentiated, ciliated inside throughout its length. Eggs operculate, thick-shelled, not embryonated *in utero*. Excretory system not made out. Parasitic underneath scales, especially below lateral line, of marine teleosts.

Type species: *Lepidodidymocystis irwini* n. g., n. sp. in *Menticirrhus nasus*; N. Mazatlan. Forebody 0.53-0.82 $\times$ 0.13-0.32 mm, hindbody 3.6-5.1 $\times$ 2.44-3.58 mm; eggs 12-15 $\times$ 9-11 μ .



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- ISHII, N. 1935. Studies on the family Didymozoidae (Monticelli, 1888). *Jap. J. Zool.* 6(2):279-335.
- YAMAGUTI, S. *Systema Helminthum*, Vol. I, revised and enlarged. (In press.)
- . Digenetic Trematodes of Hawaiian fishes. (In press.)

December 16, 1969

←

Figures 1 to 4. *Lepidodidymocystis irwini* n. g., n. sp. Fig. 1. Holotype, lateral view; Fig. 2. Paratype 16, lateral view of entire forebody and part of hindbody; Fig. 3. Paratype 7, general view of forebody and acetabulum; Fig. 4. Paratype 7, ventral view of anterior extremity of forebody.

Abbreviations used in figures: A acetabulum; C cecum; E esophagus; ER egg reservoir; F longitudinal furrow on concave side of hindbody; FB forebody; GP genital pore; HB hindbody; M metraterm; N nerve; O ovary; OS oral sucker; P pharynx; T testis; U uterus; VD vas deferens; VT vitellarium.

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TULANE STUDIES IN ZOOLOGY AND BOTANY

Volume 16, Number 2

February 25, 1970

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THE COACHWHIP SNAKE, *MASTICOPHIS FLAGELLUM* (SHAW): TAXONOMY AND DISTRIBUTION

LARRY DAVID WILSON

*Department of Biology, University of
Southwestern Louisiana, Lafayette, Louisiana 70501*

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THE COACHWHIP SNAKE, *MASTICOPHIS FLAGELLUM*
(SHAW): TAXONOMY AND DISTRIBUTION¹

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ABSTRACT

The taxonomy and distribution of *Masticophis flagellum* (Shaw) are discussed. The use of the generic name *Masticophis* instead of *Coluber* and the relationship of

the species *flagellum* to the other species within the genus *Masticophis* are briefly considered.

Six subspecies recognized previously by other authors are retained, and *fuliginosus* Cope is resurrected from synonymy for another subspecies. The concept of the subspecies *cingulum* is modified. A discussion of color pattern variation is included under each subspecies heading. The types of variation illustrated by the

¹ This work was completed in partial fulfillment for the degree of Doctor of Philosophy at Louisiana State University, Baton Rouge, Louisiana.

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color pattern are discussed, and so are intraspecific relationships.

The variation exhibited by the nonpattern characteristics is summarized and analyzed for sexual, ontogenetic, geographic, and individual significance.

Available information on distribution and habitat preference is reviewed.

INTRODUCTION

The coachwhip snake, *Masticophis flagellum*, is a wide-ranging North American species that exhibits considerable pattern variation. It has not been reviewed in its entirety since Ortenburger's (1928) revision of the genera *Masticophis* and *Coluber*. Ortenburger had approximately 400 specimens of *M. flagellum* available to him; in contrast I have examined more than five times as many. I recognize seven subspecies, three of which have been described since 1928. I have studied variation in most of the characters normally utilized in taxonomic work on snakes at the specific level, with emphasis on color pattern. These characters have been analysed for possible geographic, sexual, ontogenetic, and individual differences.

During the course of this study I have examined 2195 specimens of *Masticophis flagellum* from the following institutional and private collections:

AC	Alabama College
AMNH	American Museum of Natural History
ANSP	Academy of Natural Sciences of Philadelphia
ASDM	Arizona-Sonora Desert Museum
AU	Auburn University
BCB	Bryce C. Brown Collection, Strecker Museum, Baylor University
BYU	Brigham Young University
CAS	California Academy of Sciences
CHM	Charleston Museum
CM	Carnegie Museum
CU	Cornell University
DEH	Donald E. Hahn, private collection
EAL	Ernest A. Liner, private collection
FSU	Florida State University
HC	Howard College
INHS	Illinois Natural History Survey
JFC	Joseph F. Copp, private collection
JPC	Janalee P. Caldwell, private collection
JRD	James R. Dixon, private collection
KLW	Kenneth L. Williams, private collection
KU	University of Kansas Museum of Natural History
LACM	Los Angeles County Museum
LPI	Louisiana Polytechnic Institute

LSUMZ	Louisiana State University Museum of Zoology
MCZ	Museum of Comparative Zoology
MGFCM	Mississippi Game and Fish Commission Museum
MMH	M. Max Hensley, private collection
MISU	Mississippi State University
MSU	Michigan State University
NCSM	North Carolina State Museum
NLSC	Northeastern Louisiana State College
NMSU	New Mexico State University
NSU	Nevada Southern University
NTSU	North Texas State University
OSU	Oklahoma State University
PM	Philip Medica, private collection
RAT	Robert A. Thomas, private collection
SDSNH	San Diego Society of Natural History
SM	Strecker Museum
TCWC	Texas Cooperative Wildlife Collection
TNHC	University of Texas Natural History Collection
TU	Tulane University
UAHC	University of Alabama Herpetological Collection
UAZ	University of Arizona
UCM	University of Colorado Museum
UF	University of Florida Collections
UG	University of Georgia
UIMNH	University of Illinois Museum of Natural History
UM	University of Miami
UMMZ	University of Michigan Museum of Zoology
UNM	University of New Mexico
USL	University of Southwestern Louisiana
USM	University of Southern Mississippi
USNM	United States National Museum
UU	University of Utah

Scale counts were made in accordance with customary methods. Ventrals were counted using the method of Dowling (1951b), and so were scale reductions (Dowling, 1951a). Because of extreme variability in the temporal series, the number of scales on each side of the head was totaled as a single number.

Snout-vent length was measured from the tip of the snout to the posterior edge of the anal plate. Tail length was measured from the posterior edge of the anal plate to the tip of the tail.

Unless otherwise noted, the color pattern descriptions are based on preserved material, although I have made use of whatever living material was available.

Brackets are used in the text to indicate where a qualifying statement of mine has been made within a quotation.

I have used brief synonymies for the sub-

species discussed by Ortenburger (1928) and complete synonymies for those subspecies described since Ortenburger's work.

HISTORICAL SUMMARY

Coluber flagellum was described by Shaw (1802) from a plate in Catesby's "The Natural History of Carolina, Florida and the Bahama Islands." The provenance of the species was given as North America, and Shaw stated that it is "not uncommon in Carolina and Virginia." These states were regarded as the type locality by Ortenburger (1928). In 1823 Say described *Coluber testaceus* from the western portion of the range. Hallowell (1852) described *Psammophis flavigularis* from Cross Timbers, Oklahoma. The specific name *flavigularis* was used by Ortenburger for the western coachwhip, instead of *testaceus*, but most investigators have considered *flavigularis* to be a synonym of *testaceus*. Several subspecies have been described. Stejneger (1893) added *Bascanion flagellum frenatum*, from Mountain Spring, San Diego County, California. *Masticophis flagellum lineatulus* was described by Smith in 1941 from 11 miles north of San Buena Ventura, Chihuahua, Mexico. *Masticophis flagellum ruddocki* was described by Brattstrom and Warren in 1953 from Kern County, California. Lowe and Woodin added a sixth form, *Masticophis flagellum cingulum*, in 1954, based on specimens from Moctezuma, Sonora, Mexico.

Ortenburger (1928) was the first investigator to review the genus, and, in his excellent paper, he recognized three subspecies of *flagellum* (*flagellum*, *flavigularis*, and *frenatum*). He considered *piceus*, a name formerly applied to black individuals of *frenatum*, as a distinct species. But much more material has since accrued and three additional subspecies have been described. It is now possible to outline the range of each race with considerable accuracy, and to delineate the areas of intergradation between subspecies. Also, the considerably greater amount of specimens now available makes it possible to analyze the variation within the species with greater accuracy.

VALIDITY OF THE GENUS *Masticophis*

Considerable controversy exists in the literature as to whether or not the snakes

grouped under *Masticophis* should be considered as generically distinct from the snakes of the genus *Coluber*. In his monograph, Ortenburger (1928) discussed what he considered to be the distinguishing characteristics between *Masticophis* and *Coluber*. These included differences in the number of maxillary teeth, the type of scale reduction formula, the number of ventrals, subcaudals, and supralabials (including the number of supralabials entering the orbit, usually a function of the number of supralabials), certain characteristics of hemipenial structure, and the head width-head length ratio.

The severest critics of the use of the generic name *Masticophis* were Bogert and Oliver (1945). They cited Stuart's (1934) difficulty in deciding whether his new species *ortenburgeri* belonged to the genus *Masticophis* or *Coluber*. Stuart stated that the type specimen agreed with members of the genus *Masticophis* in having a similar scale reduction pattern, but, on the contrary, it agreed with members of the genus *Coluber* in its hemipenial structure. *Coluber ortenburgeri* has recently been shown to be the southernmost representative of and synonymous with *Coluber constrictor oaxaca* (= *C. c. stejnegerianus* auct.) (See Etheridge, 1952; Stuart, 1963; Wilson, 1966). In addition, during the preparation of my paper on Mexican *Coluber* (*op. cit.*), I examined the holotype of *Coluber ortenburgeri* and found it to be somewhat aberrant. The complete scale reduction in this specimen is:

$$\begin{array}{r} 19 \frac{3+4(5)}{3+4(5)} \quad 17 \frac{3+4(70)}{3+4(70)} \quad 15 \frac{6+7(129)}{6+7(139)} \\ \quad \quad \quad 14 \frac{\quad}{+7(129)} \quad 15 \frac{\quad}{\quad} \quad 14 \end{array}$$

This specimen has neither a typical *Coluber* nor a typical *Masticophis* scale row pattern, but it more closely resembles *Coluber constrictor*. Dunn (1933) believed that the specimen of *Coluber oaxaca* (= *C. c. oaxaca*) from Colima, Mexico that he discussed demonstrated a similarity to *Masticophis* in scale row reduction and number of supralabials. As I have stated previously (Wilson, 1966, p. 45), I believe this scale reduction pattern to be aberrant. The number of supralabials (eight) is, indeed, the

same as that seen in *Masticophis*, but eight supralabials is also characteristic of the western forms of *Coluber constrictor* (i.e., *mormon* and *oaxaca*); seven is characteristic of the more eastern forms. The mean number of supralabials increases gradually from east to west. Populations of *Coluber constrictor* in the eastern portions of Louisiana, for example, have a lower mean number of supralabials than those from the western portions of the same state (Wilson, unpublished manuscript). Use of characters exhibited in limited portions of the range of *Coluber constrictor* would not appear to be a valid criterion for demonstrating that *Masticophis* and *Coluber* are congeneric, nor are aberrant characters.

Inger and Clark's (1943) attempt to subdivide the cumbersome genus *Coluber* (*sensu lato*) has also met with criticism. Bogert and Oliver (1945) stated that these authors "attempt to partition the genus *Coluber* (in its broadest sense) on the sole basis of scale reduction patterns." This is not strictly the case because Inger and Clark used the number of supralabials entering the orbit and the presence or absence of enlarged basal spines on the hemipenis as supportive characters. Although I would agree that the subdivision of or the erection of a generic taxon, if based on a single character, is ill advised, I also believe that Inger and Clark's system contributes to a better understanding of the relationships of this group of snakes. As I have stated (Wilson, 1967, p. 269), the genus *Coluber* (*sensu lato*) is an unwieldy assemblage of snakes, many of which are only distantly related to and are even generically distinct from *Coluber constrictor*, the type species of the genus. The range of characters exhibited collectively by the species now grouped in the genus *Coluber* is very wide and indicative of an unnatural grouping. The *Coluber* complex admittedly needs further study, and the relationships of its many components may not become clear until investigations are made on skeletal anatomy, hemipenial structures, blood proteins, and behavior on a world-wide basis. To retain the species of the genus *Masticophis* in the already unwieldy *Coluber* would require inclusion also of the other New World racer genera, i.e., *Dryadophis*, *Drymobius*, *Leptodrymus*, and *Dendrophidion*, which are certainly less distinct from

Masticophis and *Coluber constrictor* than are the Old World *Coluber dorri* and *Coluber dipsas*. For these reasons I continue to use the name *Masticophis* for the whip-snakes in general and for the species *flagellum* in particular.

THE *flagellum* GROUP OF *Masticophis*

In his review of *Masticophis* Ortenburger (1928) divided the genus into two sections, the *taeniatus* group and the *flagellum* group. His *taeniatus* group included *M. aurigulus*, *M. barbouri*, *M. lateralis*, *M. ruthveni* (= *M. taeniatus ruthveni*), *M. schotti* (= *M. taeniatus schotti*), *M. semilineatus* (= *M. bilineatus*), *M. taeniatus girardi*, and *M. taeniatus taeniatus*. This group is not pertinent to the present study and will not be discussed further.

Ortenburger's *flagellum* group included *M. anthonyi*, *M. flagellum flagellum*, *M. f. flavigularis* (= *M. f. testaceus*), *M. f. frenatum* (= *M. f. piceus*), *M. lineatus* (= *M. striolatus*), *M. mentovarius*, and *M. piceus* (= *M. f. piceus*). This arrangement has seldom been challenged, and I see no reason for changing it, except to shift some names because of priorities. Smith (1941), who discussed the Mexican forms of the genus, presented a phylogeny that did not differ significantly from that of Ortenburger insofar as the division of the constituent species into two groups is concerned. Smith, however, suggested that *mentovarius* is similar to the basic stock from which the remainder of the species developed. Ortenburger, on the other hand, postulated that the two groups arose from a "... hypothetical progenitor of the genus *Masticophis*." It is my opinion that a proto-*mentovarius* was not the basic form and that, furthermore, Smith's phylogeny represents the relationships of the species of the genus *Masticophis* at the present time level.

Without adequate paleontological data it is futile to speculate on the age of certain species, but it is more logical to assume a progenitor of the genus that diverged to form two groups: (1) a banded or unpatterned form (the *flagellum* group), and (2) a striped form (the *taeniatus* group). *Masticophis mentovarius* appears to be a derivative of *striolatus* that migrated southward to invade Central and South America. It is likely that the peculiar fusion of the



Figure 1. *Masticophis flagellum flagellum* (CHAS 6722) from Vaiden, Carroll County, Mississippi.

fourth and fifth supralabials is a derived character, inasmuch as all the other members of the genus have two supralabials entering the eye, as do the members of the genus *Coluber*.

A similarity in pattern ties *mentovarius* to *striolatus*. Most likely, another derivative of *striolatus* is *M. anthonyi*, found only on Isla Clarión in the Revillagigedo Island group (Ortenburger, 1928; Brattstrom, 1955). These three species form a compact group that is distinct from all the subspecies of *Masticophis flagellum*, except for *lineatulus*, in having a lineate dorsal pattern composed of a stripe (or a dot in the case of *anthonyi*) on each scale. The pattern of *lineatulus*, however, appears to have been derived separately from that of the *striolatus* subgroup, because the juveniles are typically banded across the neck, as is the case in the young of the other subspecies of *flagellum*. Juveniles of *lineatulus* are identical with juveniles of *M. f. testaceus* in this respect.

COMPOSITION OF THE SPECIES

Masticophis flagellum

Smith and Taylor (1945) listed six subspecies of *Masticophis flagellum* (five Mexican subspecies and one extralimital form, *M. f. flagellum*). Since that time two additional subspecies (*cingulum* and *ruddocki*) have been described, and two subspecies have been removed. Bogert and Oliver (1945) demonstrated sympatry between *Masticophis striolatus* (= *Coluber striolatus striolatus* of Bogert and Oliver and *Mastico-*

phis flagellum lineatus of Smith and Taylor) and *Masticophis flagellum cingulum* (= *Coluber flagellum piceus* of Bogert and Oliver and *Masticophis flagellum piceus* of Smith and Taylor) in southern Sonora. They also stated that "the snake described by Smith (1943, p. 448) as *Masticophis flagellum variolosus*, if it proves to be valid, should be placed as a subspecies of *Coluber striolatus*." Zweifel (1960), in his study of the herpetofauna of the Tres Mariás Islands, discussed the validity of Smith's *variolosus* and concluded that "... differentiation in number of ventral scales alone is not an adequate basis for the recognition of an endemic insular subspecies. Whether *variolosus* should be recognized or not depends on the significance attached to slight but possibly consistent difference in lip pattern, in the apparent absence of more consistent differences. To recognize the subspecies would place undue emphasis on slight variation in a species not otherwise subject to variations sufficiently consistent for it to be considered polytypic, unless it proves to be conspecific with *M. mentovarius*. Hence, *variolosus* should be relegated to the synonymy of *lineatus*." Webb (1960) presented evidence confirming the specific status of *M. striolatus*. Further confirmation has been presented by Fugler and Dixon (1961) and Smith and Van Gelder (1955).

Thus, *Masticophis flagellum* presently contains six subspecies (*cingulum*, *flagellum*, *lineatulus*, *piceus*, *ruddocki*, and *testaceus*). *Masticophis striolatus* is now recognized as a distinct monotypic species. There remains,

however, the possibility that *striolatus* may be conspecific with *M. mentovarius* (Webb, 1960; Zweifel, 1960).

SUBSPECIES ACCOUNTS

Masticophis flagellum flagellum (Shaw) Eastern Coachwhip

- Coleber flagellum* Shaw, 1802: 475
Coleber testaceus: Harlan, 1826: 348
Psammophis flagelliformis: Holbrook, 1842: 11
Masticophis flagelliformis: Baird and Girard, 1853: 98
Masticophis flavigularis: Baird and Girard, 1853: 99 (part)
Herpetodryas flagelliformis: Duméril and Bibron, 1854: 210
Herpetodryas flavigularis: Günther, 1858: 118 (part)
Masticophis flagelliformis testaceus: Jan, 1863: 65 (part)
Bascanium flagelliforme flagelliforme: Cope, 1875: 40
Bascanium flagelliforme testaceum: Yarrow, 1875: 542 (part)
Bascanium flagelliforme: Cope, 1877: 64
Bascanium flagelliforme: Smith, 1882: 636
Coleber flagelliformis testaceus: Garman, 1883: 43 (part)
Bascanium flagelliformis testaceus: Duméril and Bocourt, 1886: 705
Zamenis flagelliformis: Boulenger, 1893: 389 (part)
Zamenis flagellum flagellum: Cope, 1900: 789 (part)
Zamenis flagelliforme: Ditmars, 1912: 218
Coleber flagellum flagellum: Stejneger and Barbour, 1917: 79 (part)
Masticophis flagellum flagellum: Ortenburger, 1923: 2

Holotype.—None designated. The original description by Shaw (1802) consisted primarily of information supplied by Catesby (1731-43). Shaw stated "it is a native of North America, and not uncommon in Carolina and Virginia." Schmidt (1953) restricted the type locality to Charleston, South Carolina.

Diagnosis.—A subspecies of *Masticophis flagellum* characterized by a dark to very dark brown anterior dorsal coloration and a tan to dark brown posterior dorsal coloration. The venter is dark brown anteriorly, grading to cream posteriorly (Fig. 1).

Range.—Southeastern United States from North Carolina south to and including all of Florida, west to eastern Texas, north to Missouri and southern Illinois, including the eastern half of Oklahoma and Kansas (Fig. 2).

Description.—The only information given

by Shaw (1802) was that this snake "is a very long and slender species, measuring from four to six feet or more in length: its color is a uniform dusky brown, palest beneath."

The following color pattern description is from a live female specimen (LSUMZ 9679) collected beside the Red River at the south city limits of Alexandria, Rapides Parish, Louisiana and measuring 1029 mm in head-body length. The anterior portion of the dorsum is very dark velvety brown. This color grades into pinkish brown on the posterior portion of the body and tail. Along the middle of the body, at intervals of about 100 mm, are a series of light bands about 40 to 50 mm long. They are orange brown dorsally and brownish gray laterally. There are about three or four of these bands, the last of which gives rise to a middorsal stripe-like area that is somewhat lighter than the lateral area. The venter is grayish brown on the neck with light orange flecks grading to cream posteriorly with an overtone of orange flecks. This orange coloration is darker on the lateral edges of the ventrals. The underside of the tail is pinkish orange. The head is dark velvety brown above. There is an orange spot on the right parietal. The lateral part of the head is grayish brown anteriorly, becoming brown on the temporals. There is a light spot on the upper preocular. The chin is grayish brown with white blotches on all scales. There are a few orange flecks on the gulars. The iris is dark brown except for an orange ring around the pupil.

Discussion.—Meristic and mensural data for this subspecies, based on 241 males and 207 females, may be summarized as follows: supralabials 7 to 9, infralabials 8 to 13, preoculars 2 or 3, postoculars 1 to 3, loreal 0 to 3, ventrals in males 188 to 212, ventrals in females 186 to 207, subcaudals in males 100 to 122, subcaudals in females 91 to 123, dorsal scale rows 19-17-11 to 19-17-15. Body length in males of all ages ranges from 291 to 1600 mm, in females of all ages 331 to 1520 mm. Total length in males of all ages ranges from 373 to 2074 mm, in females of all ages 436 to 1983 mm. Tail length/total length ratios in males ranges from 0.220 to 0.275, in females 0.217 to 0.300.

There is a considerable amount of pattern

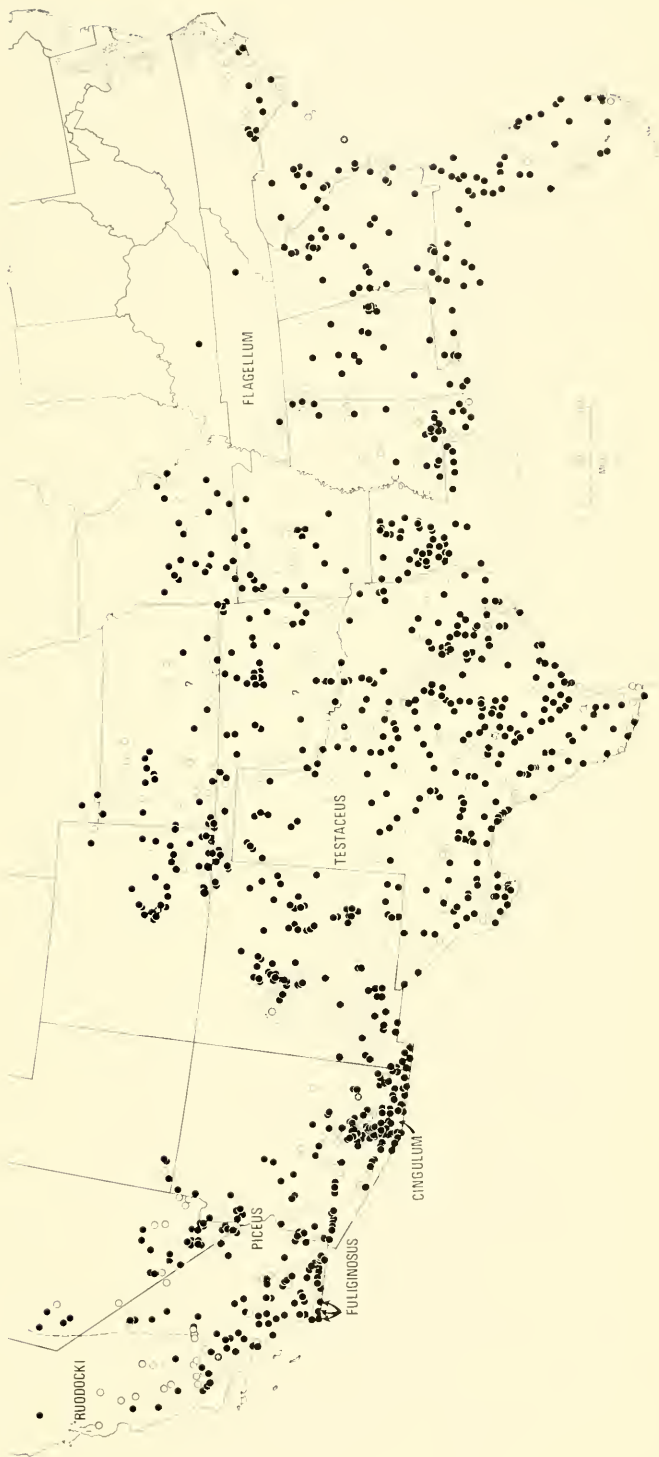


Figure 2. Distribution of *Masticophis flagellum* in the United States. Solid circles represent localities for specimens examined, open circles literature records, and stars type localities.

variation in the nominate subspecies. This subspecies exhibits an ontogenetic color change. Juveniles of *M. f. flagellum* have a pattern similar to the young and adults of *M. f. testaceus*. The dorsum is some shade of tan with narrow brown to dark brown bands on the neck and forebody, which diminish gradually in intensity posteriorly. The head is light brown or tan, with white outlining the dorsal scales, and with a dark brown area on the posterior portion of the internasals and prefrontals, on most of the supraoculars and frontal, and on the anterior, lateral, and posterior portions of the parietals. The side of the head is light brown to tan with cream spots on most scales. The chin is cream, with light brown pigment between the junction of the infralabials and the chin shields. The venter is uniform cream, except for a double row of brown spots on the neck.

As the snake increases in size the dorsal pattern on the anterior part of the body becomes uniformly dark as the result of a darkening of the existing brown or tan coloration on each scale and the invasion of the pale lateral areas of each scale by the same color. The dorsal surface of the head becomes uniformly dark by loss of the white scale borders and by a darkening of the light areas on the head. The side of the head becomes darker in an anterior to posterior direction. The chin becomes uniformly dark by the deepening of the existing brown color and a progressive invasion of that color into the light cream areas. The spots situated on the anterior portion of the venter begin to darken and enlarge. As the snake grows older and larger, these spots fuse together and still later they fuse with the lateral extension of the dorsal ground color to form the uniformly dark, anterior ventral coloration of the adult.

This description of the ontogenetic color pattern changes in *flagellum* is generalized; some individuals of this subspecies may reach a certain level in the development of the color pattern at a smaller or larger size than others. For example, in LSUMZ 16772 from Caddo Parish, Louisiana (625 mm in snout-vent length), and LSUMZ 16773 from Sabine Parish, Louisiana (621 mm), the former is much paler dorsally than the latter. The juvenile markings are still evident on the head of LSUMZ 16772 and the

spotting on the venter is more clearly defined. These two snakes were collected only a few miles apart.

A juvenile *flagellum* (OSU 483) with a curious pattern is available from Lake Carl Blackwell in Payne County, Oklahoma. This specimen, which measures 540 mm in total length, entirely lacks the typical neck bands. Instead, each of the dorsal scales, especially on the anterior portion of the body, has a concentration of darker pigment toward the center of the scale, giving the impression of a broad, diffuse stripe on each dorsal scale row.

The dorsal coloration of adults of *Masticophis f. flagellum* ranges from a completely pale tan dorsum with narrow, dark brown crossbands to one almost completely black dorsally. The most widespread type of coloration has been described above.

There are disjunct populations in northern and central Florida and southern Georgia, the adults of which are characterized by a pale tan dorsum with narrow, dark brown crossbands. A specimen of this phase (LSUMZ 18527) that I collected on 30 March 1968 on St. George Island, Franklin County, Florida, was tan dorsally with very dark brown pigment on the posterior edges of the internasals and prefrontals, the posterior one-half of the frontal, most of the supraoculars except for the extreme anterior portion, and the anterior and posterior portions of the parietals. There is some dark brown pigment on the neck arranged in the form of indistinct bands. The first band is the best developed and is about four scales wide. Ventral coloration is cream with a triangular extension of the dorsal ground color onto the lateral edges of the ventrals and some tan and dark mottling on the neck. The chin is white, heavily mottled with tan and dark brown pigment. The specimen is an adult male, measuring 1280 mm in snout-vent length.

This color phase is known from the following localities in Florida (Fig. 4): Alachua County, 1 mi. NE Archer (UF 9656); Clay County, 3 mi. S Middleburg (UIMNH 25699), Gold Head State Park (TCWC 10781); Duval County, near Jacksonville (UMMZ 67807); Escambia County, Pensacola (MCZ 98); Franklin County, St. George Island (LSUMZ 18527); Gulf County, 2 mi. S Wewahatchka (UF 6546);



Figure 3. Distribution of *Masticophis flagellum* in Mexico. Explanation as for Figure 2.

Jackson County, 1.5 mi. W Campbellton (AU 2037); Lake County, Tavares (UF 113), Leesburg (UF 2456); Leon County, east of Tallahassee (FSU 116); Liberty County, 6 mi. S, $\frac{1}{2}$ mi. E Bristol (UF 10083-1, 10083-2); Marion County, Fort McCoy (AMNH 23100); Orange County, Orlando (SDSNH 36740); Putnam County, road between Interlachen and Grandin (MCZ 67179); Washington County, 1 mi. N Ebro (LSUMZ 16860). In addition, Charles W. Myers (*in litt.*) informed me that two similar pale-phased specimens of *flagellum* escaped from him at the two following localities: Franklin County, 6 mi. S, $9\frac{1}{2}$ mi. W Carrabelle, near Green Point, and Liberty County, 18 mi. NNW Carrabelle on Florida Hwy. 67. The following records are available from Georgia: Baker County, near Newton, Pineland Plantation (CM 40196-7), 3 mi. N Newton (BYU 22188), Itchwa Plantation (UG 206); Baldwin County, Milledgeville (MCZ 286); Brantley County, 20 mi. SE Waycross (UMMZ 92793); Decatur County, 4 mi. SW Bainbridge (INHS 7612); Long County,

10 mi. SE Thomasville (TCWC 11945), 1 mi. S Thomasville (TCWC 11943), 3 mi. NW Metcalf (TCWC 11944); Wilcox County, Benhill Fishery (UG 262). Charles W. Myers also informed me (*in litt.*) that he saw a DOR specimen of this phase $9\frac{1}{2}$ mi. N, 5 mi. W Bainbridge on U.S. Hwy. 27, Decatur County, Georgia. He stated that the specimen "was also uniformly light colored but probably not as pale as those from Florida . . ." In addition, I have seen one specimen of this phase (NCSM 1966) from Rose Hill, Duplin County, North Carolina.

Even excluding this pale phase, the dorsal coloration of adults tends to be paler in Florida than in other portions of the range (Fig. 5); the darkest animals occur in Missouri, northwestern Arkansas, and eastern Oklahoma (Fig. 6). In dealing with an animal that has a color pattern consisting of an evenly graded change in color from one end of the body to the other it is difficult to devise an objective system for evaluating this color pattern. Variation in *M. f. flagellum*, therefore, is more difficult to discuss

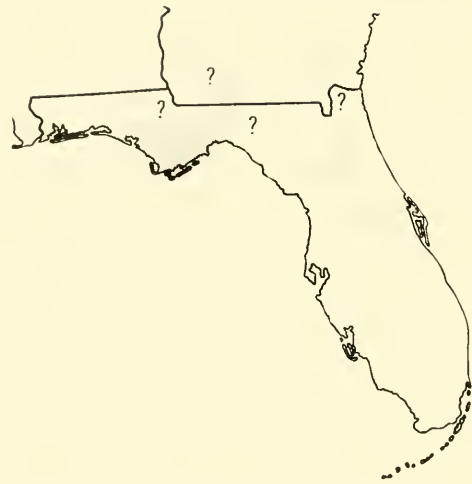


Figure 4. Distribution of the pale phase of *Masticophis flagellum flagellum* in Florida and surrounding areas.

than that of any other subspecies. In recording color notes on specimens, I have made an arbitrary judgment regarding the intensity of the color present and the extent to which the anterior portion of the body is covered by dark pigment.

An estimate of the amount of dark pigment was made on the basis of a fraction of the total body length, i.e., 1/4, 1/3, 1/2, 2/3, or 3/4. In terms of this crude method the following statements can be made (Table 1). Specimens from Florida are pre-

TABLE 1

Percentage of specimens of *Masticophis f. flagellum* exhibiting various amounts of dark pigment on the anterior portion of the body. The amount is expressed as a fraction of the total length.

Area	Fraction of Body Covered by Dark Pigment				
	1/4	1/3	1/2	2/3	3/4
Florida	68	16	16	0	0
North and South Carolina	12	71	17	0	0
Georgia, Alabama, and Mississippi	26	39	30	0	5
Louisiana, Kentucky, Tennessee, and eastern Texas	0	20	50	20	10
Arkansas, eastern Oklahoma, eastern Kansas, and Missouri	0	5	48	33	14

dominantly pale, usually one fourth or less of the body is covered with dark pigment. The extent of dark pigment on the body increases clinally from Southeast to northwest, those specimens from Arkansas, Oklahoma, Kansas, and Missouri being darkest. In addition, there is also a tendency for specimens from the southeastern and eastern portions of the range to be tan on the posterior portion of the body and for those from the northwestern and western portions of the range to be reddish brown to dark reddish brown on the posterior portions of the body (Table 2). The color of the pos-



Figure 5. *Masticophis flagellum flagellum* from Sanibel Island, Lee County, Florida.

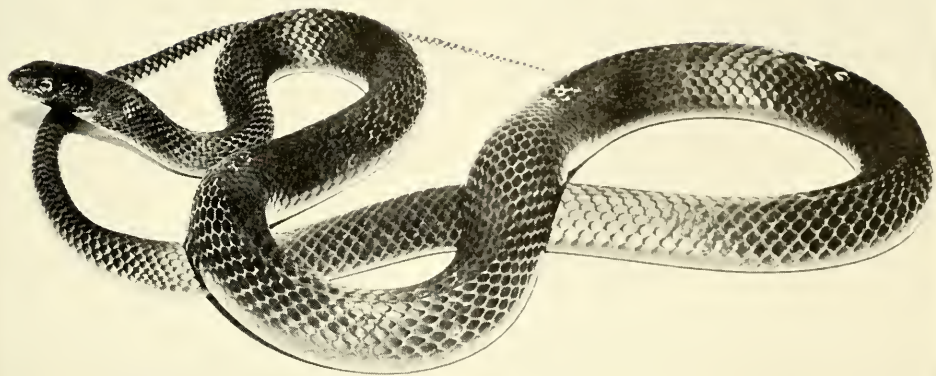


Figure 6. *Masticophis flagellum flagellum* from Salina Creek, 2 miles S Salina, Mayes County, Oklahoma.

terior portion of the body normally ranges from tan through light brown, brown, and dark brown to black. I have seen only one specimen, however, that was black posteriorly (OSU 3244 from Okmulgee County, Oklahoma).

Occasional specimens throughout the range of *flagellum* have a series of light bands across the body (Fig. 7). These bands range from four to ten scales in length and range in number from one to eight in any one snake. Some specimens (especially several from Mississippi, Louisiana, North

Carolina, and eastern Texas) have very distinct bands that are tan in color in contrast with the dark to very dark brown areas that surround them and extend completely across the dorsum. These bands may be either unicolorous or bisected transversely by a narrow dark brown band through the center. Other specimens show only slight evidence of this light banding, which is confined to the mid-dorsal and one or two paravertebral rows of dorsal scales. I have seen banded specimens from every state within the range of *flagellum* except South Carolina, Kentucky, and Illinois (only one adult from each of the last two states). There is no geographical continuity to this type of pattern, inasmuch as specimens from the same general area may be banded or nonbanded. For example, in a series of twelve adults from Bladen, Hoke, Richmond, and Scotland counties in south-central North Carolina, eight specimens are banded and four are not.

My interpretation of the zone of intergradation between *M. f. flagellum* and *M. f. testaceus* is at variance with that given by Brown (1950). Examination of the material from eastern Texas demonstrates that the southern portion of the intergrade zone (Fig. 2) is fairly wide, as indicated by Brown, but lies farther to the east. My reason for this conclusion is that specimens from Colorado County (KU 1459, 1463), and Matagorda County (MCZ 19895,

TABLE 2
Percentage of specimens of *Masticophis f. flagellum* exhibiting various colorations of the posterior portion of the body.

Area	Tan	Light brown	Brown	Dark brown
Florida	91	9	0	0
Georgia	58	31	11	0
Alabama	41	41	18	0
Mississippi	83	13	4	0
South Carolina	80	20	0	0
Kentucky, Tennessee, and Illinois	75	25	0	0
Louisiana	47	16	35	2
Eastern Texas	19	33	31	17
Arkansas	19	25	37	19
Eastern Oklahoma	2	28	42	28
Eastern Kansas	0	66	17	17
Missouri	10	19	52	19

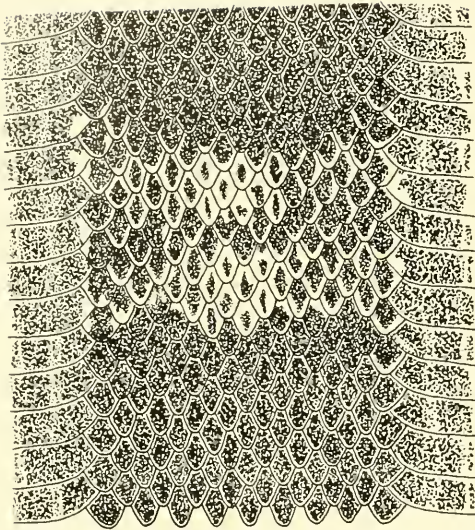


Figure 7. Pattern at midbody of *Masticophis flagellum flagellum*, (CM 24649) from 1.7 miles S Boles, Scott County, Arkansas.

UIMNH 28508, USNM 32770-71) show no approach to *flagellum* in coloration. Also, I have seen three specimens from Galveston Island, two of which (UIMNH 25811, UNM 8849) are typical *testaceus* whereas the other (UIMNH 28510) shows some influence from *flagellum*. Specimens from Bell County, from which Brown listed one specimen with no specific locality, are typical *testaceus* (KU 72914, SM 7009 and 7033, UNM 9207). Another specimen (KU 72915) from Bell County may show some influence from *flagellum*. On the eastern edge of the intergrade zone two specimens (TCWC 196, TNHC 33876) from Harris County are intergrades and two others (ANSP 10871, LSUMZ 14146) show no approach to *testaceus*. Most of the 14 specimens from Brazos County that I have examined are *flagellum*, but five (TCWC 195, 2482, 4751, 14522; UAZ uncatalogued) show influence from *testaceus*. North of Dallas and Tarrant counties the zone of intergradation apparently becomes very narrow. I have seen a single specimen from Wise County (USNM 83127), most likely the same specimen examined by Brown, and I agree with him that it is a *testaceus* showing no approach to *flagellum*. I have been fortunate in having available a series of recently collected specimens from

Denton County. All four adults from this county (NTSU 193, 238, 268; TNHC 26773) definitely have a *flagellum* pattern with no influence from *testaceus*. One juvenile (NTSU 223) is unquestionably a *flagellum* as it has already begun development of the typical adult pattern of this subspecies. Two other juvenile specimens (NTSU 186, 207) look like *testaceus*. Neither specimen, however, has the dark head markings of juvenile *flagellum*. I do not know if juveniles of the two races can be distinguished in an area of intergradation.

The zone of intergradation between *flagellum* and *testaceus* in Oklahoma and Kansas is largely conjectural. A single specimen (KU 8389) from Love County, Oklahoma, is a *flagellum*. I have seen no specimens between this county and Payne County, Oklahoma, to the north. Most of the specimens I have seen from Payne County are *flagellum*, but four (MCZ 61175; OSU 482, 485-86) show influence from *testaceus*. The sample from Noble County to the north includes some of the darkest specimens of *flagellum* that I have examined. I have seen no intergrade specimens from Kansas, and the zone of intergradation that I depict (Fig. 2) is based on Smith (1950).

The zone of intergradation follows approximately the ecotone between the pine and hardwood forests of eastern Texas and the prairie and hardwood forests of east-central Texas (Austroriparian and Texan biotic provinces of Raun, 1965). According to Raun the major trees of the Austroriparian biotic province include longleaf pine (*Pinus palustris*), loblolly pine (*Pinus taeda*), yellow pine (*Pinus echinata*), post oak (*Quercus stellata*), blackjack oak (*Quercus marilandica*), red oak (*Quercus falcata*), sweetgum (*Liquidambar styraciflua*), and wax myrtle (*Myrica cerifera*). The major trees of the Texan biotic province are post oak, blackjack oak, and hickory (*Carya* spp.), and mesquite (*Prosopis juliflora*), a recent invader.

Masticophis flagellum testaceus (Say)
Western Coachwhip

Coluber testaceus Say, 1823: 48

Psammophis flavigularis Hallowell, 1852: 178
(type, ANSP 5388, Cross Timbers, Oklahoma)

Masticophis flavigularis: Baird and Girard, 1853: 99 (part)

Herpetodryas flagelliformis: Günther, 1858: 118 (part)
Coryphodon testaceus: Günther, 1858: 108
Masticophis testaceus: Baird, 1859: 43
Masticophis flagelliformis testaceus: Jan, 1863: 65
Masticophis flagelliformis testacea: Jan, 1867: livr. 20, pl. 6, fig. 2
Bascanium flagelliforme testaceum: Yarrow, 1875: 542 (part)
Bascanium flagelliforme bicinctum Yarrow, 1883: 153 (type, USNM 11814, Old Fort Cobb, Texas)
Coluber flagelliformis testaceus: Garman, 1883: 43 (part)
Bascanium flagelliformis: Duméril and Bocourt, 1886: 705 (part)
Zamenis flagelliformis: Boulenger, 1893: 389 (part)
Zamenis flavigularis: Günther, 1895: 120 (part)
Bascanium flagelliforme: Dugès, 1896: 481
Zamenis flagellum flagellum: Cope, 1900: 799 (part)
Bascanium flagellum: Bailey, 1905: 46
Bascanium flagellum frenatum: Bailey, 1913: 35
Coluber flagellum flagellum: Stejneger and Barbour, 1917: 79 (part)
Masticophis flagellum flavigularis: Ortenberger, 1923: 2
Coluber flagellum picus: Van Denburgh, 1924: 217

Holotype.—Lost. Originally in the collection of the Academy of Natural Sciences of Philadelphia. Type locality: junction of Turkey Creek with the Arkansas River, 12 mi. W Pueblo, Pueblo County, Colorado (Maslin, 1953).

Diagnosis.—A subspecies of *Masticophis flagellum* characterized by a light tan or light brown (Fig. 8) to pinkish red dorsum with darker narrow crossbands on the neck and a double row of dark spots on the otherwise immaculate cream belly.

Range.—South-central United States from western Kansas, extreme southwestern Nebraska, and eastern Colorado, south through eastern New Mexico and all of Texas except for the eastern pine forest. In Mexico the western coachwhip occurs in eastern Coahuila, Nuevo León, Tamaulipas, eastern San Luis Potosí, and extreme northern Veracruz (Figs. 2 and 3).

Description.—The following description is based on LSUMZ 18688, an adult female from 10 miles SE Colorado Springs on the grounds of Fountain Valley School, El Paso County, Colorado, collected 18 May 1967 by Robert M. Stabler. This specimen is from relatively near the type locality. Scutellation: supralabials 8-8, 4th and 5th entering the

orbit; infralabials 11-10, four touching the anterior chin shields, fifth the largest; loreal 1-1; preoculars 2-2; postoculars 2-2; temporals 6-6; scale reduction pattern

$$\begin{array}{r} 19 \frac{3+4(9)}{3+4(10)} \quad 17 \frac{3+4(121)}{3+4(116)} \\ 15 \frac{7+8(134)}{7+8(131)} \quad 13 \frac{7=7+8(138)}{7+8(131)} \\ 14 \frac{7+8(141)}{\quad} 13; \end{array}$$

ventrals 197; tail incomplete. Head-body length 1159 mm.

The dorsum is Dragon's-blood Red (color terminology based on Ridgway, 1912) on the nape grading to Light Coral Red posteriorly. The dark crossbands on the neck are near Liver Brown. The venter is Light Coral Red. The spots on the ventral surface of the neck are Dragon's-blood Red, the remaining spots are yellowish cream. The top of the head is near Hay's Russet (reddish brown). The anterior edge of each dorsal head scale is lighter (pink). The side of the head is reddish brown and the temporals are outlined with pink. A cream spot is present on the upper preocular. The chin is white with mustard yellow and reddish orange blotching.

Discussion.—Meristic and mensural data for this subspecies, based on 365 males and 313 females, may be summarized as follows: supralabials 7 to 9, infralabials 8 to 12, preoculars 2 or 3, postoculars 1 to 3, loreal 1 to 2, ventrals in males 173 to 204, ventrals in females 180 to 203, subcaudals in males 95 to 121, subcaudals in females 93 to 117, dorsal scale rows 19-17-12 to 19-17-15. Body length in males of all ages ranges from 263 to 1480 mm, in females 279 to 1270 mm. Total length in males of all ages from 375 to 1780 mm, in females 376 to 1655 mm. Tail length/total length ratios in males range from 0.195 to 0.272, in females 0.224 to 0.272.

Maslin (1953) noted the presence of red individuals of *Masticophis flagellum* in the Arkansas River Valley of eastern Colorado. He stated that this phase occupied a distinct area in Colorado and demonstrated that the name *Coluber testaceus* Say, 1823, was applicable to this form. Prior to this date,

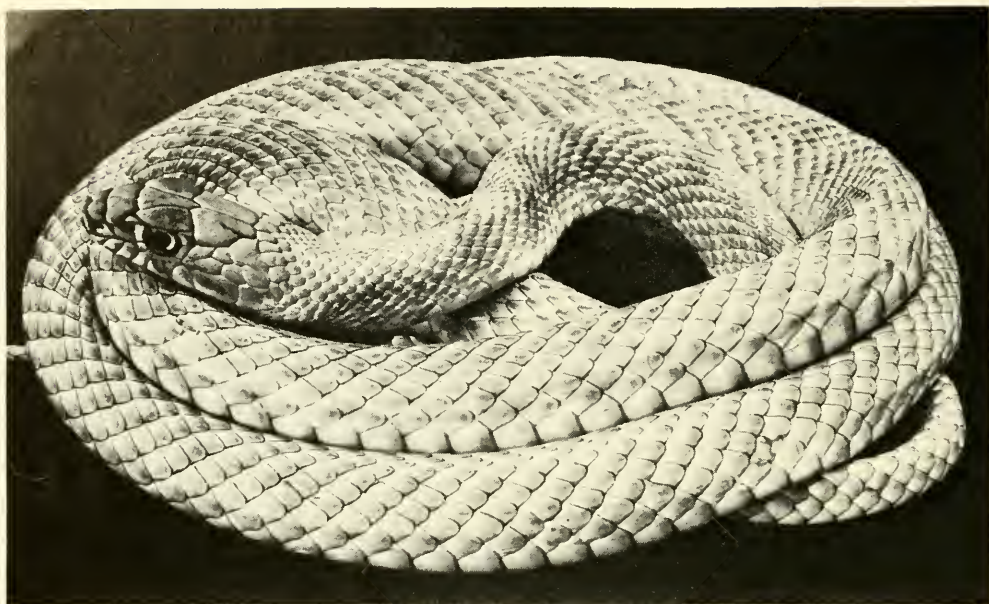


Figure 8. *Masticophis flagellum testaceus* (LSUMZ 12878) from Meade County State Lake and Park, Meade County, Kansas.

however, Schmidt and Smith (1944) and Jameson and Flury (1949) had noted the presence of red specimens of *Masticophis flagellum* in Trans-Pecos Texas. Schmidt and Smith (*loc. cit.*) stated "the red racer is a familiar snake on the desert areas surrounding the Chisos [Mountains]." Jameson and Flury (*loc. cit.*) also stated that "two of our specimens have a distinct reddish color anteriorly and ventrally while another is dark red." They noted, however, that "other specimens show the more typical yellow-tan dorsal color." Minton (1959) and Axtell (1959) likewise noted the presence of reddish-colored whipsnakes in the Big Bend National Park and the Black Gap Wildlife Management Area in Brewster County, Texas.

Recently, I became aware of a similar population of red *testaceus* in eastern New Mexico. I have seen specimens from $\frac{1}{4}$ mile N Logan (JRD 9518) and the vicinity of Tucumcari (UAZ uncatalogued), Quay County, 10 miles NW Ramon (UNM 172) and 8 miles ENE Vaughn (JRD 9519), Guadalupe County, and about 65 miles NW Roswell, Lincoln County (NMSU 2213). I examined the University of Arizona specimen just a few days after it was preserved.

The dorsum was reddish orange with about ten narrow darker bands on the neck and forebody. The venter was cream with a light reddish orange overtone and a double row of indistinct reddish orange spots on the neck.

The existence of these disjunct populations (Fig. 9) of reddish-colored individuals in eastern Colorado, eastern New Mexico, and western Texas, and the presence of normally pigmented individuals in at least the Trans-Pecos populations, makes Maslin's (1953) arrangement untenable. The name, therefore, of the wide-ranging tan form (as well as the red phase of this subspecies) should be *Masticophis flagellum testaceus* (Say).

The factors responsible for the existence of these red whipsnakes in at least three disjunct areas remain obscure. The shortgrass prairie of eastern Colorado and eastern New Mexico, and the desert scrub and barren flats of the Big Bend region would seem to have little in common. Thus, the occurrence of the red color phase seems not to be correlated with any vegetation type.

Considering the disjunct nature of the range of the red populations, there is no alternative to recognizing them as represent-

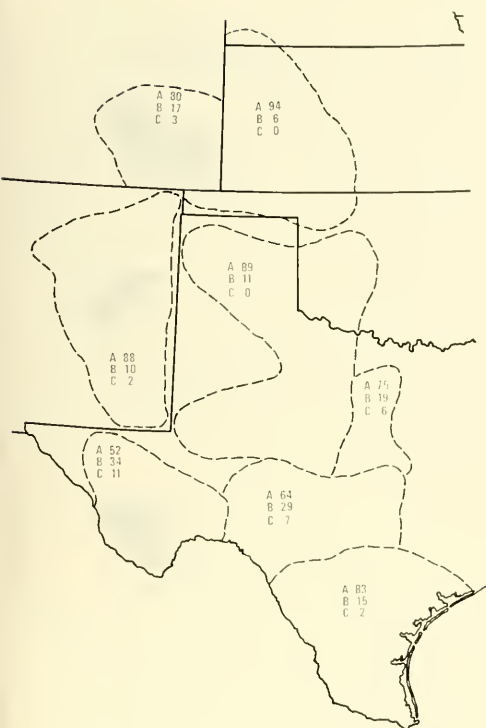


Figure 9. Distribution of the phases of *Masticophis flagellum testaceus* in the United States. Striped areas indicate the range of the red phase and the numbers within the areas outlined by a dashed line are the relative percentage values of the three pattern types of *M. f. testaceus*.

ing a color phase of the subspecies *testaceus*. The exact limits of the range of this form are difficult to plot inasmuch as the red coloration fades in preservative to the tan of typical *testaceus*. Maslin (1959) listed specimens from Baca, El Paso, Fremont, Kiowa, Las Animas, Otero, and Prowers counties, all in southeastern Colorado. In addition, Maslin (*in litt.*) stated that they occur in Bent County. In New Mexico it is known from the three counties listed above. In Texas it is found in Presidio and Brewster counties (Fig. 9).

In contrast to the pink or red coloration, the tan coloration occurs virtually throughout the range. A snake with this type of coloration was described by Hallowell (1852) as *Psammophis flavigularis*. The name *flavigularis* was used for the western coachwhip by Ortenburger (1928), who

thought that Say's (1823) description of *Coluber testaceus* as a "pale sanguineous or testaceous" snake too uncertain to warrant the use of this name. Klauber (1942, p. 93, footnote) expressed a contrary opinion, however, when he stated, "I cannot see by what line of reasoning the name *testaceus* is not applicable to this subspecies [the western coachwhip]. At the time the type specimen was collected (about July 18, 1820) the Long Expedition was at the foot of the Rocky Mountains, toward the headwaters of the Arkansas River. The description, though brief, fits no other snake found in that region. It does not fit the prairie racer, usually referred to as *C. f. flavigularis*, and this snake does occur in that vicinity. I am therefore of the opinion that the prairie subspecies should be known as *Coluber flagellum testaceus* Say, 1823."

Ortenburger (1928) noted three basic types of coloration in *M. f. testaceus*. These were: "(1) a very light brown ground color with no indication of a pattern; (2) the same general light brown ground color with numerous narrow, darker crossbands (two to three scales in width), which extend for a considerable portion of the body length; (3) few wide, dark crossbands (ten to fifteen scales in width) on either a light or dark brown ground color." Ortenburger further noted (p. 102):

"Variation in color and pattern is probably greater in this form than in any other member of the genus. When the actual distribution of the types of pattern was studied, it was found that there is a definite relation between the types of pattern and distribution. To the east throughout the region between the ranges of *flagellum* and *flavigularis* it was noticeable that there is a much greater number of specimens which possess the pattern composed of a few wide stripes. Toward the center of the range and south the unicolor light form is more numerous; to the west this again is gradually replaced by the form with many narrow stripes. Southeastern Texas seems to be the only region which does not hold to this type of distribution, as here one finds (if we can trust the locality records) a veritable mixture of all three forms. At present it does not seem that these forms should

be considered as distinct, since there are no structural characters which will support the color pattern differences, and it is believed that the locality records for southeastern Texas, if accurate enough, would show that these forms are found in distinct habitats. While lack of data at present precludes the possibility of determining definitely what it is that actually causes these differences of color pattern, there can be no doubt that definite relations of pattern to environment will be shown when the necessary data are available."

My data suggest a somewhat different interpretation. Contrary to what Ortenburger contended, the three color pattern phases of *testaceus* do not occupy discrete areas within the total range of the subspecies. Figures 9 and 10 show that the narrow-banded phase (A) is by far the most common in all areas within the range. The incidence of occurrence of this pattern type ranges from 52% to 94%. It is highest in Kansas and lowest in Trans-Pecos Texas. The incidence of the unicolor phase (B) ranges from 6% to 34%. It is lowest in Kansas and highest in Trans-Pecos Texas. The incidence of the widebanded phase (C) ranges from 0% to 20%. No specimens of this phase were found in the material from Kansas, Nebraska, Oklahoma, or the panhandle of Texas. The percentage of this phase is highest in Coahuila and Nuevo León. There are no areas other than the ones mentioned above where all three of the phases fail to occur. All three phases were present in several collections from a single county. All three pattern phases undoubtedly do occur in the red phase of this subspecies also, however, I have not seen unicolor specimens which were red at the time of examination. I have seen unicolor specimens from within the ranges of the red phase and these specimens may have been red in life.

The following is a description of the color pattern of the narrow-banded phase (based on notes made on a living specimen, now in the private collection of Janalee P. Caldwell, collected 5.8 miles NW Cotulla on Hwy. 468, LaSalle County, Texas). The dorsum is tan with a slight pink wash on the nape. The neck bands are brown, 1 to 1½ scales wide and separated by 2½ to 3 scales. The venter is cream (light yellow on

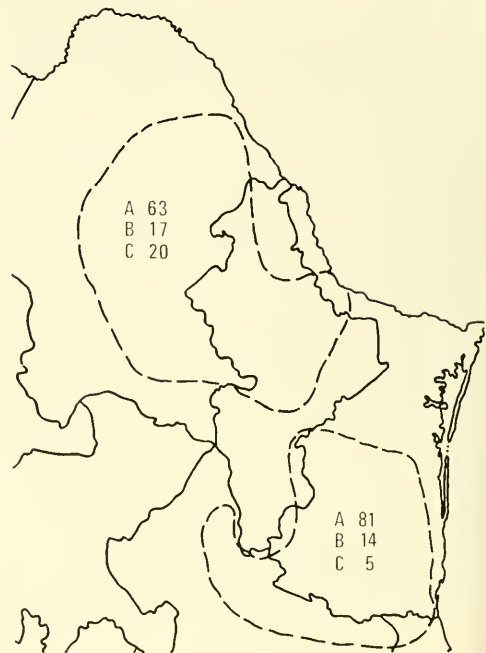


Figure 10. Percent frequency of the three pattern types of *Masticophis flagellum testaceus* in Mexico.

neck) with a double row of light brown spots on the neck. The head is tan dorsally, the scales outlined with white. The lateral area of the head is also tan with light yellow blotching on some of the scales. The chin is white with light brown blotching.

The unicolor phase is uniform light tan dorsally and cream ventrally with a double row of brown spots on the neck and forebody.

The following description is of the widebanded phase (based on TNHC 30448 from 4 miles SSW Cuatro Ciénegas, Coahuila, Mexico; Fig. 11). The dorsum is tan with about 6 brown bands, 12 to 14 scales in width. Each of these long brown bands has several narrower, darker bands within it. The throat is dark brown and there is a double row of brown spots extending posteriorly from this area. The posterior portion of the venter is cream. The chin is dark brown with cream spotting.

I can find no basis for Klauber's (1942, p. 93) statement that "*C. f. flavignularis* . . . tends to produce black (especially anteriorly) specimens in parts of New Mexico

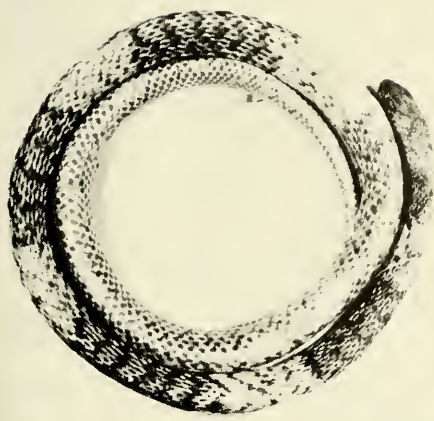


Figure 11. *Masticophis flagellum testaceus* (TNHC 30448) from 4 miles WSW Cuatro Ciénegas, Coahuila, Mexico.

and Oklahoma . . . ” Dr. Klauber stated (*in litt.*) that although he had no memory of these specimens, perhaps some note of this characteristic might have been made on his original data sheets that I sent me. Upon looking through his data I find no mention of any *testaceus* from Oklahoma having this coloration. Two specimens, however, which may have been in the University of New Mexico collection (the designation used for the specimens is “N.M.,” no numbers are given) from Bernalillo County, New Mexico, are described as “grayish black” and “light brown, somewhat darker on the head.” I have examined the entire University of New Mexico collection and have seen no specimens fitting such descriptions. Possibly fading may have taken place as it often does in snakes that have long been preserved.

Masticophis flagellum lineatulus Smith
Lined Whipsnake

Bascanium flagelliforme testaceus: Cope, 1886: 284 (part)
Masticophis flagellum flavigularis: Ortenburger, 1928: 102 (part); Dunkle and Smith, 1937: 4; Gloyd and Smith, 1942: 233
Masticophis flagellum lineatulus Smith, 1941: 394, 1943: 446; Taylor, 1944: 185, 1949: 170, 1952: 811; Smith and Taylor, 1945: 95, 1950: 327; Brown, 1950: 168; Schmidt, 1953: 189; Stebbins, 1954: 495, 1966: 150; Conant, *et al.*, 1956: 12, 1965: 18; Grant and Smith, 1959: 55; Cochran, 1961: 196; Fowle, 1965: 71

Holotype.—USNM 105292. Type locality: 11 miles N San Buena Ventura, Chihuahua, Mexico.¹

Diagnosis.—A subspecies of *Masticophis flagellum* characterized by a tan or light gray dorsum with each dorsal scale on the anterior portion of the body having a central longitudinal dark streak (Fig. 12). The posterior portion of the venter and the underside of the tail are salmon pink (this color does not fade in preservative).

Range.—Extreme southwestern New Mexico and southeastern Arizona south through most of Chihuahua (except the southwestern portion), southwestern Coahuila, eastern Durango, northern Zacatecas, and western San Luis Potosí (Figs. 2 and 3).

Description of Holotype.—Scutellation: supralabials 8-8, fourth and fifth entering the orbit; infralabials 9-10, four touching the anterior chin shields, fifth the largest; loreal 1-1; preoculars 2-2; postoculars 2-2; temporals 7-8; scale reduction pattern

$$\begin{array}{rcl} & 3 + 4 \text{ (11)} & 3 + 4 \text{ (119)} \\ 19 \frac{\quad}{3 + 4 \text{ (13)}} & 17 \frac{\quad}{3 + 4 \text{ (121)}} & \\ & 7 + 8 \text{ (120)} & 7 + 8 \text{ (142)} \\ 15 \frac{\quad}{\quad} & 14 \frac{\quad}{\quad} & \\ & 6 + 7 \text{ (173)} & \\ 13 \frac{\quad}{\quad} & 12; & \end{array}$$

ventrals 195; tail incomplete. Body length is 1616 mm (Smith reported 1481 mm, apparently in error), the incomplete tail measures 335 mm.

Smith (1941) described the color pattern of the holotype as follows: “Head light yellowish brown, darker toward posterior sutures; sides of head light yellowish brown, with a lighter area in the preocular, loreal, nasal and rostral; a dark, rounded spot in center of nasal [I find this spot to be in the rostral, not the nasal]; supralabials white below a line about even with posterolateral border of seventh labial and middle of subocular labials.

“Dorsal ground color light yellowish brown, becoming more reddish toward middle of body, posteriorly mostly salmon red; all anterior dorsal scales with a central longitudinal black streak, which becomes

¹ Original description stated “south” (Cochran, 1961, p. 196).

more spot-like on scales in middle of body, barely indicated on posterior scales, as the black spots become less distinct, the red areas become more distinct, the posterior scales being mostly red (with a little black near tip), with a white (cream) base; dorsal surface of the tail is even more strongly marked with salmon red.

"Posterior edge of mental and broad areas near the sutures between the infralabials and chin shields, black-marked brown; a double row of black spots beginning with anterior ventral scales; posteriorly these spots becoming mixed with red and soon mostly red and very little black; anterior ground color of belly yellow, this color extending onto lower dorsal scale rows; toward middle of belly this color is largely replaced by salmon red, and posteriorly the belly is entirely red, with the double row of black spots faintly indicated; ventral surface of tail mostly red, the bases of the scales lighter (cream)."

Discussion.—Meristic and mensural data for this subspecies; based on 29 males and 20 females, may be summarized as follows: supralabials 8 or 9, infralabials 9 to 12, preoculars 2, postoculars 2, loreal 0 to 3, ventrals in males 183 to 199, ventrals in females 185 to 197, subcaudals in males 99 to 109, subcaudals in females 95 to 103, dorsal scale rows 19-17-12 to 19-17-13. Body length in males of all ages ranges from 249 to 1270 mm, in females 290 to 1281 mm. Total length in males of all ages ranges from 332 to 1650 mm, in females 386 to 1616 mm. Tail length/total length ratios in males range from 0.213 to 0.262, in females 0.207 to 0.260.

I have examined the entire type series of this subspecies and find that some comment is necessary. Seven of the specimens (USNM 14279, 104675, 104676, 105292, 1988, 14283, 46355) are typical *lineatulus*. Two (USNM 12676, 26151), from Guanajuato and "Mexico," respectively, are juvenile *Masticophis striolatus*. Another specimen (USNM 8429) from "New Mexico," considered by Smith (1941) to be a possible intergrade between *lineatulus* and *flavigularis* (= *testaceus*), is a juvenile and cannot be allocated to subspecies. Smith apparently considered USNM 1989 from Co-bre Mines, New Mexico, as typical of the subspecies; I would identify it as an intergrade between *lineatulus* and *testaceus*, as

I would USNM 4388 from Laguna, Valencia County, New Mexico. Both have striping on the dorsal scales but lack red color of the posterior ventrals and the subcaudals.

There is very little pattern variation in adults of this subspecies, in marked contrast to all other subspecies of *Masticophis flagellum* with the exception of *M. f. rud-docki*. The color pattern of the specimens I have examined conforms very closely to the description given by Smith (1941). He failed to mention, however, the coloration of the nape, which is light yellow to yellowish-tan. This coloration occupies an area of from six to twelve scales posterior to the parietals. This area is distinctly set off from the lineate coloration which follows it. There is some slight variability in the anterior extent of the salmon red ventral coloration and the extent of coverage of individual ventrals. In some specimens the posterior half of each ventral is salmon red or pink and the anterior half is cream. In others the whole scute is salmon pink or red. The ventral, as well as the dorsal, coloration varies ontogenetically and is discussed below.

Specimens from Zacatecas are not so brightly colored as those from Durango, Coahuila, and San Luis Potosí. All three of the adult specimens I have seen (UMMZ 123251-52; AMNH 82156) lack bright yellow coloration on the anterior ventrals, and the salmon pink coloration on the posterior portion of the body and underside of the tail is not nearly so bright or extensive in distribution. The nape band, which is light yellow in more typical adult *lineatulus*, is yellowish tan in the Zacatecas specimens. Conant (1965) also mentioned this in his discussion of AMNH 82156, which he reported as the first record for the state of Zacatecas.

The record for this subspecies from 6 miles S Artesia, Eddy County, New Mexico (Gehlbach, 1956), obviously is an error, inasmuch as the area is inhabited by *testaceus*.

Juveniles of *Masticophis flagellum lineatulus* are indistinguishable from those of *M. f. testaceus*, that is, in both races the dorsal pattern consists of narrow (less than one scale long to one scale long), uniformly dark bands separated by lighter interspaces of variable length (usually 2 to 3 scales in

length). This differs from the type of color pattern seen in juveniles of the *piceus* group, in which the bands are longer (usually about 3 scales long) and are bounded anteriorly and posteriorly by an irregular, narrow dark line. The dorsal surface of the head in juvenile *lineatulus* is relatively uniform in coloration (unlike the head pattern of *flagellum*, and the other subspecies in the *testaceus* group), and the anterior portion of the venter is marked with a double row of brown spots. There is a nonbanded area of variable length (9 to 11 scales long) on the nape.

By the time the animal has reached a snout-vent length of approximately 500 mm, the adult pattern has begun to develop. The unique subcaudal and posterior body color is one of the first of the adult characteristics to appear (indications of this coloration are shown by AMNH 82154 which has a snout-vent length of only 305 mm). The salmon color develops first along the posterior edge of the subcaudals and posterior ventrals. Also, the yellow coloration of the anterior region of the venter develops at about 500 mm.

The lineate pattern of the dorsum of the adults develops from the banded juvenile pattern by an intensification of the dark markings on the scales within the juvenile bands and by the progressive development of longitudinal stripes on the scales between the bands. Therefore, as the animal matures the salmon color becomes brighter, covers more area on each scale, and progressively obscures the banded juvenile pattern.

As the lineate pattern of the dorsum becomes more well defined, the nape area becomes more noticeable by its lack of pattern. Also, it is dull yellow in contrast to the brown ground color of the dorsum.

At about 900 mm the dorsum of the posterior region of the body is infused with the same salmon color that is found on the posterior ventrals. This salmon color occupies the posterior half of each scale, leaving the anterior half tan in coloration.

In adult animals (above 950 mm) each ventral on the posterior portion of the body is almost completely covered with salmon pink pigment. The posterior half of each subcaudal is also salmon-colored, the anterior half being white. The remainder of

the venter, except for the first few ventrals (which are cream) is bright yellow. Each of the dorsal scales has a more or less centrally located black stripe. The nape is dull yellow.

Intergradation between *M. f. lineatulus* and *M. f. testaceus* in New Mexico takes place over a broad area from Valencia and Bernalillo counties southwestward to southern Catron County and southeastward to western Otero County. The southern limits of this intergrade zone are unknown because of a lack of specimens from northwestern Chihuahua. Within New Mexico, however, there is decreasing indication of the *lineatulus* pattern to the north. Specimens from Hidalgo, Luna, and Dona Ana counties show a great amount of influence from *lineatulus* to the south.

The following color pattern is of a living specimen from Las Cruces, Dona Ana County (LSUMZ 10519). The dorsum is brownish gray anteriorly, grading to brown posteriorly. A series of indistinct bands is present on the neck and forebody. Each scale on the anterior portion of the body has a black line extending through the center. The lateral edges of the posterior body scales are yellow. There is also an indistinct broken line on scale row 2 on the posterior portion of the body. The base of the scales in row 1 is tinged with orange. The nape has a distinct yellowish tinge. The venter is cream to white with a double row of dark brown spots that become diffuse on the forebody and are gradually replaced by light orange. This coloration becomes more prominent posteriorly, and on the posterior portion of the body and tail forms the posterior border of each scale. The head is light brownish gray above with darker blotching on some head scales. The lateral area of the head is similarly colored with light yellow blotches on the posterior nasal, loreal, and upper preocular. The supralabials are white except for the posterodorsal corner of each, which is grayish brown. The chin is white with brown blotching.

Some New Mexico specimens from Dona Ana County show no pink or orange coloring on the ventrals or subcaudals and so approach *testaceus* in this respect. A single specimen from Catron County (UNM 9312) has no pink on the subcaudals but has the typical *lineatulus* striping on the

dorsum. A specimen from Grant County (UNM 8422) is similar but has a pink tinge on the posterior edge of the subcaudals. A specimen from Otero County (NMSU 1796) has only slight indications of striping on the dorsum and is otherwise like *testaceus*. A single specimen from Sierra County (UNM 435) has light dorsal streaking and some light pink coloration on the posterior ventrals and subcaudals.

Specimens from Socorro, Valencia, and Bernalillo counties show a varying degree of influence from *lineatulus*. Some specimens more closely resemble *testaceus*, others *lineatulus*. From its description, the specimen (TNHC 4487) discussed by Gehlbach (1965) appears to be an intergrade. He stated "the recent specimen, an adult male, 1070 mm in total length, has longitudinal lines on the dorsal scales but retains anterior crossbands and lacks the diagnostic red subcaudal color."

Specimens from El Paso County, Texas, also show characteristics of both *lineatulus* and *testaceus*. I have seen two such specimens (KU 72910, UMMZ 117769). Robert G. Webb stated (*in litt.*) "strangely, the coachwhips in the El Paso area are hard to come by—the only one I have seen, which was a DOR, and is now a skeleton in our collections, I would call an intergrade; although the specimen was torn up badly, the posterior part of the body (dorsally and ventrally) had the characteristic magenta color of *lineatulus*. This DOR specimen is from Jueco Tanks, about 25 miles east of El Paso." Also, Strecker (1915) gave the following information: "Several coachwhips from El Paso County combine the characters of the two western subspecies, *frenatum* and *piceus*, having narrow crossbands in front and the underparts bright pink in color." These words, written twenty-six years before *lineatulus* was described, give a fairly accurate and succinct description of a *lineatulus* × *testaceus* intergrade.

In Arizona the intergrade zone becomes narrower and more complex as three subspecies intergrade in southern Cochise, southern Pima, and Santa Cruz counties, *M. f. lineatulus* from the southeast, *M. f. cingulum* from the south, and *M. f. piceus* from the north. Influence from *lineatulus* is seen in specimens from the vicinity of

Portal and Rodeo on the eastern side of the Chiricahua Mountains. These individuals do not differ essentially from specimens seen from Hidalgo County, New Mexico. A specimen from 5-8 miles S San Simon in the San Simon Valley (UAZ uncatalogued) is similar to those from near Portal and Rodeo except that it lacks the salmon subcaudal color, and the lines on the dorsal scales are not particularly dark. It does not, however, show any influence from *piceus*. I have seen specimens from the Sulphur Springs Valley and one from the San Bernardino Valley which show influence from *lineatulus* and a varying amount of influence from *piceus* and *cingulum*. Two specimens (both uncatalogued specimens in the UAZ collections) appear to be intergrades between *piceus* and *lineatulus*. A specimen from 28 miles NW Willcox, at the north end of the Sulphur Springs Valley (UAZ uncatalogued), shows more influence from *lineatulus* than from *piceus*. The following description is of this specimen, seen soon after it had been preserved. The dorsum is brown with a dark streak down the center of each scale. Posteriorly these streaks become less prominent. There is an indication of banding on the neck as in *piceus*. The venter is white anteriorly grading to cream. The posterior edge of the ventrals of the posterior region of the body and the subcaudals are salmon pink.

The other specimen is from the Willcox Playa and shows more influence from *piceus*. Its color pattern (in preservative) consists of a brown dorsum (more reddish brown on the neck and forebody) with a few of the dorsal scales having *lineatulus*-type striping. Neck bands are of *piceus* type. The venter is cream anteriorly with a double row of dark brown spots grading to light rust on the posterior portion of the body and the underside of the tail. The head has a typical *piceus* coloration.

A specimen from 4 miles S Dos Cabezas (ASDM 655) looks very similar to typical banded *cingulum*, but there is a slight indication of *lineatulus* influence in neck banding. Another specimen from 5.6 miles N Bernardino (AMNH 75130) has a *lineatulus* nape band and a *piceus*-type head pattern. Banding of a *piceus* type is present on the neck but *lineatulus* striping is also present. Lowe (1964: 20) mentioned the intrusion of typical Chihuahuan Desert

vegetation into parts of the San Simon and Sulphur Springs valleys and it is evidently through these avenues that the influence of *lineatulus* has spread into Cochise County.

M. f. piceus and *M. f. cingulum* intergrade along the area of contact between the elements of the Sonoran Desert and the Desert-Grassland ecotone (see Lowe, 1964). Intergrades have been examined from the Palo Alto Ranch, along the Tucson-Nogales Highway (U.S. 89) and from about Continental south to Arivaca Junction. I have also seen intergrades from the eastern slope of the Huachuca Mountains, and specimens which look like *cingulum*, *piceus*, and *cingulum* $\times$ *piceus* intergrades from the region of Fort Huachuca.

Masticophis flagellum cingulum is known in Arizona from several localities in the oak woodland between the Patagonia and Pajarito mountains and occurs as far north in Santa Cruz County as Tubac (SDSNH 32504). I have seen one specimen from Peña Blanca in the foothills of the Pajarito Mountains, also an oak woodland habitat. Another specimen was examined from 8 miles S Arivaca (UAZ uncatalogued), and I collected a DOR specimen 11 miles NNE Arivaca, Pima County, in mesquite grassland. *M. f. cingulum* is also found in desert grassland near Sonoita between the Santa Rita and the Patagonia mountains. It is also found in the region between Palominas and Douglas.

Masticophis flagellum piceus is an inhabitant of the Sonoran Desert in Arizona and its distribution conforms well to the outline of that vegetational complex as described by Shreve and Wiggins (1964), except that it occurs somewhat farther east and south. It also extends north into the Mohave Desert. The type locality of *M. f. piceus* (black phase), Camp Grant, is not included in the Sonoran Desert, as outlined by Shreve and Wiggins. This snake may provide additional evidence for a zoological redefinition of the eastern edge of the Sonoran Desert (Lowe, 1955), but it does not occur as far east as Lowe has placed the boundary.

It is difficult to decide exactly where the zone of intergradation between *testaceus* and *lineatulus* in southwestern New Mexico should be drawn. I examined a series of specimens from Hidalgo and Cochise coun-

ties (three specimens), and three from Chihuahua and Coahuila side by side, and found that if they were arranged in linear order according to snout-vent length the gradation in color pattern was not even. The Mexican specimens showed more characteristics of the subspecies *lineatulus*.

The New Mexico and Arizona specimens showed fewer characteristics of *lineatulus* and more influence from the subspecies *testaceus*. I consider, therefore, that populations of *Masticophis flagellum* from the southwestern portion of New Mexico and extreme eastern Cochise County, Arizona, represent intergrades between *lineatulus* and *testaceus*, albeit much closer to *lineatulus*.

Masticophis flagellum piceus (Cope)

Red Racer, Western Black Racer

Bascanium flagelliforme testaceum: Cope, 1875: 40 (part)

Bascanium flagelliforme piceum Cope, 1875: 40

Bascanion flagelliformis: Duméril and Bocourt, 1886: 704

Zamenis flagelliformis: Boulenger, 1893: 389 (part)

Bascanion flagellum frenatum Stejneger, 1893: 208 (type: USNM 16340, Mountain Spring, Colorado Desert, San Diego County, California)

Bascanion piceum: Van Denburgh, 1896: 1006

Zamenis flagellum flagellum: Cope, 1900: 789 (part)

Zamenis flagellum piceus: Cope, 1900: 804

Bascanium flagellum: Meek, 1906: 15 (part)

Zamenis flagelliformis frenatus: Ditmars, 1907: 288

Zamenis flagelliformis piceus: Ditmars, 1907: 288

Coluber flagellum frenatus: Grinnell and Camp, 1917: 190

Coluber flagellum piceus: Stejneger and Barbour, 1917: 79

Masticophis piceus: Ortenburger, 1923: 2

Masticophis flagellum frenatus: Ortenburger, 1923: 2

Masticophis flagellum frenatum: Klauber, 1926: 144

Masticophis flagellum piceus: Tanner, 1927: 57

Holotype.—USNM 7891. Skin of an adult female (?) from Camp Grant (= Fort Grant), Graham County, Arizona, collected by E. Palmer.

Diagnosis.—A subspecies of *Masticophis flagellum* with two color phases, one black and the other red. The former is completely black dorsally and salmon pink to red posteroventrally. The red phase is pink to red with relatively wide crossbands on the

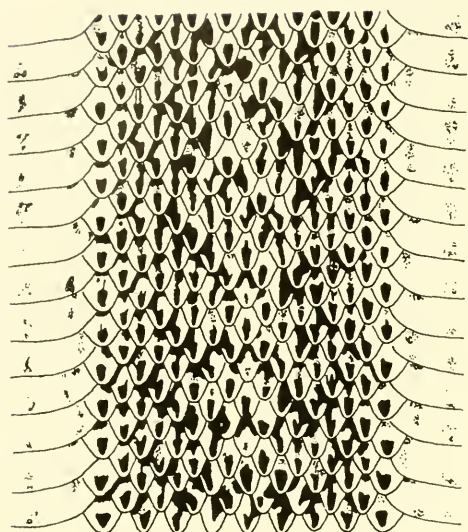


Figure 12. Pattern on the anterior portion of the body of *Masticophis flagellum leucatus* (MSU 4448) from 3 miles E Las Nieves, Durango, Mexico.

neck that range in color from that of the general ground color (in which case the anterior and posterior edges are outlined with darker pigment) to black (Fig. 13).

Range.—Arizona south of the Mogollon and Coconino plateaus, excepting Santa Cruz County and southern and southeastern Cochise County, then north through Mohave County, Arizona, into Washington County, Utah. From there the range extends westward into southern and western Nevada and southern and southeastern California exclusive of the San Joaquin Valley. In Mexico this subspecies occurs only in the Gran Desierto of northwestern Sonora and that part of Baja California del Norte that lies east of the San Pedro Martir Mountains and north of Bahia San Felipe (Figs. 2 and 3).

Description of Holotype.—Scutellation: supralabials 8-8, fourth and fifth entering the orbit; infralabials 9-10, four touching the anterior chin shields, fifth the largest; loreal 1-1; preoculars 2-2; postoculars 2-2; temporals 8-7; ventrals 194; caudals 106 (tip of tail broken off).

The holotype of *Bascanium piceum* Cope is a representative of the black phase of this subspecies. Inasmuch as the colors of the living animal have been lost or subdued by

its long preservation the following description of a specimen without precise locality data and purchased from a dealer is given. The dorsum is black except for a few small flecks of salmon pink on the frontal and parietals. The venter is black anteriorly becoming increasingly salmon pink. The lateral $\frac{1}{4}$ of each ventral is black. The distal end of the dorsum of the tail is salmon pink with black flecks. The head is black except for a white spot on the upper preocular, the first and fourth infralabials, and a few gulars.

Discussion.—Meristic and mensural data for this subspecies, based on 232 males and 145 females, may be summarized as follows: supralabials 7 to 9, infralabials 9 to 12, preoculars 2 or 3, postoculars 2 or 3, loreal 1 or 2, ventrals in males 183 to 205, ventrals in females 184 to 205, subcaudals in males 97 to 120, subcaudals in females 96 to 115, dorsal scale rows 19-17-12 to 19-17-14. Body length in males of all ages ranges from 294 to 1290 mm, in females 300 to 1154 mm. Total length in males of all ages ranges from 393 to 1668 mm, in females 400 to 1541 mm. Tail length/total length ratios in males range from 0.221 to 0.326, in females 0.233 to 0.298.

The more widespread red phase of the subspecies *piceus* was described by Stejneger as *Bascanium flagellum frenatum*. The scutellation data for its holotype (USNM 16340) is: supralabials 8-8, fourth and fifth entering the orbit; infralabials 11-9, four touching the anterior chin shields, fifth the largest; loreal 1-1; preoculars 2-2; postoculars 2-2; temporals 5-6; scale reduction pattern

$$\begin{array}{rcl} 19 & \frac{3+4(10)}{3+4(11)} & 17 \frac{3+4(110)}{3+4(112)} \\ 15 & \frac{7+8(112)}{14} & \frac{7+8(128)}{13}; \end{array}$$

ventrals 194; subcaudals 114.

The coloration of the type specimen is faded, and therefore the following description is given of a specimen (LSUMZ 10058) which I collected 9 miles WNW Westmorland, Imperial County, California, on 10 August 1965. The dorsum is reddish orange anteriorly grading to pinkish tan



Figure 13. Red phase of *Masticophis flagellum piceus* from Miramar, San Diego County, California.

posteriorly. The first two neck bands are somewhat more brown than the ground color. The venter is light orange anteriorly grading to bright pink posteriorly. There are a few darker flecks on the ventral surface of the neck. The head is grayish brown dorsally and laterally. There are light markings present on the posterior nasal, loreal, preoculars, postoculars, and temporals. The temporals are tinged with pink. The chin is white with gray flecks.

The most significant aspect of color pattern variation in this subspecies is the sympatric occurrence, in certain parts of the range, of two dimorphic phases, a black and a red one. As can be seen above, these phases were originally described as distinct species and were retained at that level by Ortenburger (1928). He was of the opinion that the black and red phases differed in at least four other characteristics besides color. He stated that the black phase snake "is noticeably a stouter and larger animal than *frenatus*," that the red phase snakes take to the bushes as a means of escape, whereas black phase snakes escape into holes in the ground, that the subcaudals are more numerous in black snakes than in red ones, and, finally, that black snakes have a proportionally longer tail than the red snakes.

Smith (1941) pointed out that *piceus* is "almost beyond question, a mutant form, occurring within the range of '*frenatus*,'" and that the name *frenatus* is not available, because it is a junior secondary homonym of

Coluber frenatus (= *Elaphe frenata*) and thereby permanently rejected.

Klauber (1942), in an excellent paper on the subject, discussed the status of the black whipsnake. In this paper he showed that each of Ortenburger's alleged differences between the black and red phases was untenable. He also pointed to the existence of intermediate specimens as indicative of the conspecificity of the two forms. Furthermore, he stated that this is not the only example of color pattern variation in this subspecies, to wit "coastal San Diego specimens have black necks, while those from the desert side of the mountains and the Imperial Valley are without this dark color or it is only faintly evident."

No one seems seriously to have questioned this interpretation, with the exception of Brattstrom and Warren (1953). In their description of *Masticophis flagellum ruddocki* they stated (p. 179) "because we have described *ruddocki* primarily on the basis of color, we feel that it might be well to clarify our position on the taxonomic status of the black forms of *M. f. piceus* in Baja California and Arizona. No new additions have appeared to challenge Klauber's (1942) conclusions that the black racer (*M. piceus*) is merely a color phase of the red phase (*M. f. frenatum*) (= *M. f. piceus*). We feel that intensive study will support some of Ortenburger's (1928) observations on the distinct ecological separation of these two forms. Ortenburger, however, came to the conclusion that the black racer (*M.*

piceus) deserved specific recognition. We feel that because of the existence of a few specimens which appear to be intergrades, the black racer should only be considered a race of the red racer (*M. f. piceus* and *M. f. frenatum*, respectively). As for the black forms of southern Arizona, it is quite possible that these represent another subspecies whose closest affinities are with the black racers of Baja California. (If so, it would become *M. f. piceus* and the Baja California form named new). Such a disjunct distribution need not cause undue surprise in light of other recent works dealing with the same situation in almost the same area. We refer to the relationship between *Crotalus viridis helleri* and *Crotalus viridis cerberus* (Klauber, 1949) and to the possible relationship of *Lampropeltis zonata* to *L. doliata gentilis* (Zweifel, 1952). These authors seem to have misunderstood Klauber's paper specifically and the subspecies concept generally. Klauber rightly pointed out in his 1942 paper (p. 88) that "since there appears to be no area in which the black form is found alone, it can hardly be considered a valid subspecies." Thus, Brattstrom and Warren's statement that the intermediate specimens support the recognition of the black and red racers as subspecies of the same species is meaningless. The rest of the paragraph also has little pertinence. The situation in the whipsnakes is not at all comparable with that of *Crotalus viridis cerberus* and *C. v. helleri*, or *Lampropeltis zonata* and *L. triangulum*.

The distribution of the black phase of *piceus* (Fig. 14) is confined to south-central Arizona. I have seen specimens from as far north as 15 miles SE Florence, Pinal County, and Klauber (1942) reported a specimen from a little farther north at Florence Junction. I have seen the phase as far west as 25 miles E Gila Bend, Maricopa County, and 5 miles N Park Headquarters, Organ Pipe Cactus National Monument, Pima County; as far south as Sasabe, Pima County, and the Santa Rita Experimental Range, Pima County; and as far east as Fort Grant (= Camp Grant, the type locality of *piceus*), Cochise County.

In order to determine, at least approximately, the density of distribution of the black phase over its range I placed a 10-mile square grid over a standard highway

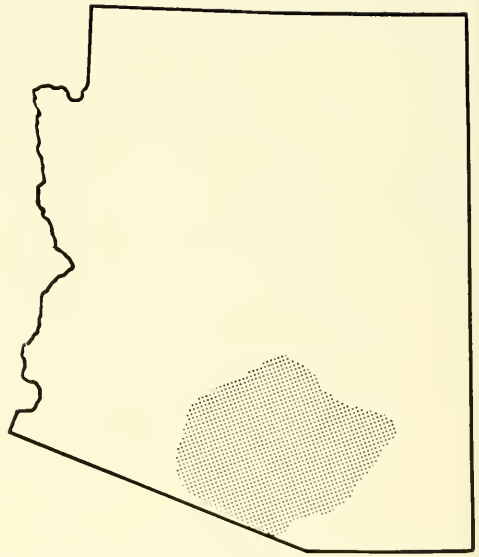


Figure 14. Distribution of the black phase of *Masticophis flagellum piceus* in Arizona.

map of Arizona and recorded the number of specimens that fell within each section of the grid. I also recorded the numbers of specimens of typical red phase *piceus* and those with intermediate coloration. Of the specimens of the black phase examined, 75% were collected within all the squares touching the square occupied by Tucson in Pima County. Beyond this area the percentages become smaller, although more black phase individuals occur west of Tucson than in other directions. The most distant record is about 110 air miles from Tucson, in the Organ Pipe Cactus National Monument (UAZ uncatalogued). Other outlying records lie between 60 and 90 miles from Tucson.

Klauber (1942) stated that black racers outnumber red ones in the vicinity of Tucson. In order to determine whether or not this is the case, I counted the numbers of the red, intermediate, and black snakes within each section of the grid from which specimens were available. My determinations made by this method corroborate those of Klauber. Within all the squares touching the square occupied by Tucson, where the black phase is most common, of the total number of *Masticophis flagellum piceus* examined, 58.9% are of the black phase, 26.3% are of the intermediate phase and

14.8% are of the red phase. It is also interesting that although the black racer inhabits an area encompassing most of Pima and Pinal counties and portions of Maricopa and Graham counties, the snakes intermediate in coloration between the black and red phases are only found within a 30-mile radius of Tucson.

A specimen of this intermediate phase (LSUMZ 10521) from the vicinity of Tucson, Pima County, was given to me by John W. Wright. The neck and forebody of this specimen are black grading to reddish-brown, speckled with black markings on some scales. The middorsal area is more red than the lateral area. The venter is black on the neck grading to pink on the rest of the venter. The head is velvety black dorsally and laterally. The chin is very dark brown with a small amount of white blotching. The eye is gold around the pupil and dark brown around the edge.

Unfortunately I have seen very few living specimens of the red phase of *piceus* and comments on color are taken from the literature. One feature of the color pattern that can be observed on preserved specimens is the difference in coloration of the neck bands. Klauber (1942) stated "coastal San Diego County specimens have black necks, while those from the desert side of the mountains and the Imperial Valley are without this dark color or it is only faintly evident." The degree of variability over the entire range of *piceus* is great. The neck bands may be the same color as the dorsum (outlined anteriorly and posteriorly by a very narrow band of darker pigment) or range from light brown or light gray through grayish brown to black. I have subdivided this continuous variation into five arbitrary categories: A. pink (essentially the same color as the dorsum), B. light gray or light brown, C. brown or gray, D. dark gray or dark brown, E. black. I have excluded those specimens having a coloration intermediate between the black and red phases. By this method a crude estimate can be made of the incidence of occurrence of each band color type in any given area (Table 3). With the exception of coastal southern California, which apparently lacks pink-banded individuals, all the neck band colors occur in every area, although one type may predominate.

Concerning the occurrence of *Masticophis flagellum* in the southwestern portion of Colorado, Maslin (1959) stated "the inclusion of this species [meaning the subspecies *piceus*] in the fauna of the state is based on reports of specimens seen in the vicinity of Mesa Verde National Park. I also saw, but failed to collect, a pale reddish-brown specimen 30 mi. W Cortez, Montezuma County, at the mouth of Yellow Jacket Canyon in June, 1958. It is possible that the form that undoubtedly occurs in this area should be assigned to *M. f. flavigularis*. But biogeographic evidence, based on the distribution of other species of reptiles, indicates that it should be tentatively recognized as *M. f. piceus* until corroboration from actual specimens is possible." Douglas (1966), who spent three years at the Mesa Verde National Park, did not mention this subspecies in his paper on the amphibians and reptiles of the park and, to my knowledge, no specimens have been collected to date. Douglas (pers. comm.) also stated that he had never heard of any red racers being found in this area. It seems unlikely that *piceus* or any subspecies of *flagellum* would occur in this area since no specimens are known from the higher elevations of northeastern Arizona and northwestern New Mexico and, indeed, the distribution of *Masticophis flagellum* seems to be limited by these higher elevations.

Masticophis flagellum ruddocki

Brattstrom and Warren

San Joaquin Whipsnake

Coluber flagellum frenatus: Grinnell and Camp, 1917: 190 (part)

Coluber flagellum piceus: Van Denburgh, 1922: 664 (part); Klauber, 1942: 88 (part)

Masticophis flagellum frenatus: Ortenburger, 1928: 112 (part)

Masticophis flagellum ruddocki Brattstrom and Warren, 1953: 177; Cunningham, 1955: 218; Conant, *et al.*, 1956: 12; Miller and Stebbins, 1964: 409; Montanucci, 1965: 278; Stebbins, 1966: 150

Masticophis flagellum piceus: Stebbins, 1954: 495 (part)

Holotype.—UCLA 6108 (specimen now in the collection of the Museum of Vertebrate Zoology, University of California at Berkeley), collected $\frac{1}{4}$ mile S of ridge at Wheeler Ridge and $1\frac{1}{2}$ miles W U.S. Hwy. 99, Kern County, California, on 12 April 1953 by James W. Warren.

TABLE 3.
Percentage of specimens of the red phase of *Masticophis flagellum piceus*
exhibiting various colorations of the neck bands.

Area	Color of neck bands				
	Pink	Light gray or light brown	Brown or gray	Dark gray or dark brown	Black
Arizona	30	25	11	9	25
Utah and Nevada	11	20	33	13	23
Desert areas of southern California	15	8	8	15	54
Coastal areas of southern California	0	3	6	8	83

Diagnosis.—A subspecies of *Masticophis flagellum* characterized by a light yellow to olive yellow dorsum with neck bands obsolete or absent (Fig. 15).

Range.—The San Joaquin and Sacramento valleys of central California from Colusa County south to Kern and San Luis Obispo counties (Fig. 2).

Description of the Holotype.—(based on data from original description). Scutellation: supralabials 8-8; infralabials 10-10; preoculars 1-1; postoculars 2-2; ventrals 197; subcaudals 105.

Brattstrom and Warren (1953) gave the following description of the color pattern (presumably in life). "The color varies from spots of Aniline Yellow on the sides of the head and neck to a solid ground color of Buffy Citrine on the sides of the body and Saccardo's Olive dorsally. The ventral color is consistently Straw Yellow (capitals are Ridgway's Color Standards, 1912), with Aniline Yellow or black on the lateral edges. The top of the head is light brown with two dark spots on the supraoculars. There is a small postocular brown stripe on the edge of the postocular and anterior temporals. The labials each have a dark spot and the anterior ventrals have Aniline Yellow spots on them. There are two faint lateral light stripes on the anterior one-third of the body. This is caused by the first scale row being yellow-tipped at its dorsal and ventral corners. There is no evidence of any neck banding."

Discussion.—Meristic and mensural data for this subspecies, based on 10 males and 6 females, may be summarized as follows: supralabials 8 or 9, infralabials 9 to 11, preoculars 2 to 4, postoculars 2, loreal 0 or 1,

ventrals in males 188 to 198, ventrals in females 191 to 198, subcaudals in males 101 to 112, subcaudals in females 102 to 108, dorsal scale rows 19-17-13. Body length in males of all ages ranges from 764 to 970 mm, in females 987 mm. Total length in males of all ages ranges from 1015 to 1323 mm, in females 1329 mm. Tail length/total length ratios in males range from 0.247 to 0.267, in females 0.257.

I have seen only 17 specimens of *rud-docki*, excluding the holotype, the identity of which is made unquestionably clear by Brattstrom and Warren (1953).

This subspecies, in common with *M. f. lineatulus*, exhibits none of the types of color pattern variation seen in the other subspecies and it has only one basic pattern. All of the specimens I have examined exhibit the coloration described for the subspecies by Brattstrom and Warren (1953), but there does seem to be some slight color variation. The dorsum ranges from yellowish tan to light olive yellow. Most specimens have at least some evidence of banding on the neck, but the bands are reduced in number, in comparison with *M. f. piceus*, or are indistinct and, in general, the same color as the dorsum. Some specimens are light tan ventrolaterally (to the level of scale row 5 or 6) and light olive yellow on the more dorsal rows. Several specimens examined have a distinct orange tinge on the neck region, both dorsally and ventrally.

The single specimen (SDSNH 26084) I have seen from the northern portion of the range (actually in the Sacramento Valley) is somewhat peculiar in having each dorsal scale with a darker central area giving the impression of a vague stripe on each dorsal scale row.

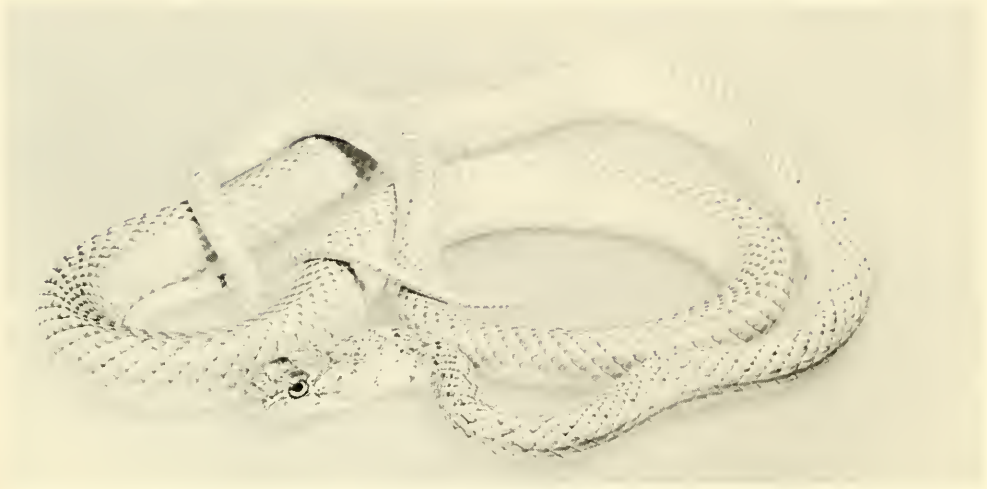


Figure 15. *Masticophis flagellum ruddocki* (UMMZ 78242) from 50 miles W Maricopa, Santa Barbara County, California.

Apparently there is some color variation in this subspecies which reflects the influence of *M. f. piceus*. Joseph F. Copp (*in litt.*) stated that "... a DOR adult that was partly picked clean by birds was noted on California 166, 14.6 mi. W of New Cuyama, and was red rather than yellow as *M. f. ruddocki* is supposed to be. When they were fresh, the two specimens in my collection from that valley [JFC 62-62 and 63-55] were also red, and the black banding on the neck is moderately evident." Stebbins (1966, pl. 30) illustrated a specimen of a coachwhip from Santa Cruz County, California, which is red. The specimen shows some neck banding but of a kind atypical for either *ruddocki* or *piceus*. The illustration closely resembles the pink phase of *M. f. testaceus*.

Intergradation with *Masticophis f. piceus* takes place in low passes through the mountains surrounding the southern end of the San Joaquin Valley. *M. f. piceus* occurs in Mohave, Great Basin, and Sonoran Desert vegetation in southern and southeastern California, extending as far north into chaparral as Los Angeles County to the west and Inyo County to the east. Intergradation may be expected anywhere along the southern end of the valley where there are areas in the mountains of sufficiently low elevation to allow contact between the two subspecies. I have seen an intergrade from 15.9 miles

W New Cuyama, Cuyama Valley, San Luis Obispo County (JFC 63-55). Another specimen (LACM 2239) from 5 miles W Arwin cutoff, 3 miles S Bina Siding, Hwy. 466, Kern County, only about 20 miles from the type locality and within the valley, shows influence of *piceus*. It is yellowish tan above with gray neck bands, which are better developed than in *ruddocki*. Five specimens were considered by Brattstrom and Warren (1953) to be intergrades between *ruddocki* and *piceus*, and the localities for them are as follows: Kern River at Bodfish (MVZ 2792), 6 mi. SSE Weldon (MVZ 56717), Weldon (MVZ 2793), Isabella (MVZ 2794), 1 mile E Onyx (UCLA 6106 = LACM 19258), and Monolith (LMK 27422 = SDSNH 27422). All localities are in Kern County, four in the Kern River-Walker Pass area (5245 ft elevation), and one in the Tehachapi Pass area (3793 ft elevation). I have seen two of these specimens (LACM 19258 and SDSNH 27422) and consider both of them to be *piceus* with no evidence of the influence of *ruddocki*. Thus, the zone of intergradation between *piceus* and *ruddocki* as pictured in Fig. 2 is largely conjectural and roughly corresponds with the location of the mountains at the southern end of the San Joaquin Valley.

The areas of intergradation between *ruddocki* and *piceus* need to be determined and

the distribution of *ruddocki* within the valley needs to be better documented.

Masticophis flagellum cingulum

Lowe and Woodin

Banded Red Racer

Bascanion flagellum frenatum: Van Denburgh, 1897: 463

Coluber flagellum piceus: Van Denburgh, 1922: 664 (part); Klauber, 1942: 88 (part); Bogert and Oliver, 1945: 363

Masticophis flagellum frenatus: Ortenburger, 1928: 112 (part)

Masticophis piceus: Allen, 1933: 11; Taylor, 1936: 490

Masticophis flagellum frenatum: Taylor, 1936: 490

Masticophis flagellum frenatum × *flavigularis*: Gloyd, 1937: 117

Masticophis flagellum piceus: Smith, 1941: 397 (part); Smith and Taylor, 1945: 95 (part); Langebartel and Smith, 1954: 134; Zweifel and Norris, 1955: 252; Stebbins, 1966: 150 (part)

Masticophis flagellum cingulum Lowe and Woodin, 1954: 247; Conant, *et al.*, 1956: 12; Fowlie, 1965: 69; Stebbins, 1966: 150

Holotype.—UAZ 672 collected at Moctezuma, Sonora, Mexico, about 2000 ft elevation, in 1951 by A. W. Ruff.

Diagnosis.—A subspecies of *Masticophis flagellum* with a highly variable color pattern. The dorsal coloration ranges from a series of wide reddish brown bands separated by narrower, paired light bands to uniform reddish brown or uniform black.

Range.—Arizona, from about midway between Tucson and Nogales, east to Douglas, and west to the region of Arivaca, thence southward to southern Sonora, including most of that state except for the Gran Desierto and the mountainous eastern portion (Figs. 2 and 3).

Description of the holotype.—Scutellation: supralabials 8-8, fourth and fifth entering the orbit; infralabials 11-12, four touching the anterior chin shields on the left and five on the right, fifth on the left and sixth on the right the largest; loreal 1-1; preoculars 2-2; postoculars 2-2; temporals 7-7; scale reduction pattern

$$\begin{array}{rcl} 19 \frac{4+5 (11)}{3+4 (14)} & 17 \frac{8+9 (113)}{13} & \\ 16 \frac{3+4 (117)}{3+4 (117)} & 14 \frac{7+8 (138)}{13} & \end{array}$$

ventrals 191; tail incomplete. Body length is 1023 mm, tail incomplete.

Lowe and Woodin (1954) described the color pattern (in life) as follows: "Mid-dorsally the dark brown ground color tends to be blackish brown, grading to dark reddish brown (near Pl. 7, J 12)¹ dorso-laterally and to lighter reddish brown (near Pl. 7, J 7) laterally. Each dorsal scale tends to be darker on its posterior portion. On the anterior body, only a few scales are edged with pink (on the anterior portion of the scale); there is a progressive increase posteriorly in amount of pink per scale. Thus pink predominates on the posterior body and tail and the darker brown is there restricted to the posterior edge of each scale.

"The upper surfaces of the head are reddish brown, distinctly darker on the supraoculars and with faint light edges to the scales. There are conspicuous pink, (Pl. 2, J 9) marks (light areas) on the labials, postoculars, preoculars, nasals, and loreal. The pink of the postnasal, loreal, and preocular is continuous and forms a 'loreal stripe' from orbit to naris. Under surfaces of the head are variously colored cream and pink with small dark brown and black spots and blotches.

"The ventral surface of the neck is dark pink (Pl. 2, J 9) being approximately the same color as the undersurface of the tail and of the gular area. The ventral surface at mid-body is a lighter pink (Pl. 2, G 8) than the neck and tail venters. The dark pink venter of the tail is near Pl. 2, J 8. The entire ventral surface is patterned by bold brown transverse cross lines adhering to the posterior margins of the ventral scutes and extending completely across them. These are commonly associated with brown blotches on the lateral margins of the scutes. In addition to the dark transverse lines on the neck, there are the commonly observed (in *M. flagellum*) bilateral row of dark blotches and spots on neck and gular region gradually fading away posteriorly.

"On the upper surfaces, there is a series of conspicuous light-colored transverse, narrow bands or cross-bars which extend completely across the lateral and dorsal surfaces of the neck and body. Their effect is to

¹ Their color terminology based on Maerz and Paul (1950).

break up the dark ground color of the upper surfaces into several large, longitudinally oblong sections. The first of these bands is approximately four scales posterior to the parietal head plates (counting scales along the vertebral line). This anterior-most band is the narrowest and most sharply defined and is approximately one and a half scales in width. The second pink band is somewhat wider, being approximately two scales in width, and, like the remainder, is less sharply delimited along its edges than is the first. The second band is approximately 12 scales posterior to the first. The third, fourth, and fifth bands are simple single transverse bands approximately like the second. The next and last three bands or band areas (sixth, seventh, and eighth) are actually narrow double bands of pink separated by a similar narrow band of dark brown ground color. The sixth band area (double band of pink) begins approximately 75 scales posterior to the head (parietals). It is separated from the seventh band area by approximately 18 scales; the seventh is similarly separated from the eighth by approximately 17 scales. There appears to be a faint trace of a ninth band area on the posterior body half where the ground color gradually becomes the uniform braided pattern of the tail.

"There is a faint, barely perceptible trace of a light longitudinal . . . line (pink) on the anterior body involving the first two scale rows. On the posterior body area, the lower scale row gradually becomes predominately pink, taking on the color of the adjacent scutes. This is concomitant with the graduation posteriorly into a 'uniform' braided whiplike pattern of light pink and brown. On the neck are traces of additional pink 'bands' which give a clue to a probably more banded neck in hatchlings and juveniles as is commonly seen in members of the *flagellum* complex."

Discussion.—Meristic and mensural data for this subspecies, based on 84 males and 41 females, may be summarized as follows: supralabials 7 to 9, infralabials 9 to 12, preoculars 1 to 3, postoculars 2, loreal 0 or 1, ventrals in males 189 to 203, ventrals in females 188 to 201, subcaudals in males 97 to 121, subcaudals in females 97 to 111, dorsal scale rows 19-17-12 to 19-17-13. Body length in males of all ages ranges from

303 to 1410 mm, in females 282 to 1186 mm. Total length in males of all ages ranges from 408 to 1850 mm, in females 371 to 1541 mm. Tail length/total length ratios in males range from 0.223 to 0.269, in females 0.226 to 0.280.

This subspecies was envisioned by its describers as ranging from Moctezuma, Sonora (the type locality), northward to Amado, Santa Cruz County, Arizona. They stated, however, that the southern, eastern, and western limits were unknown at that time. The subspecies was diagnosed as follows: "characterized by adult dark red-brown ground color on upper surfaces periodically broken by complete transverse, narrow, light-colored (pink) cross-bands which break the ground color into large, dark, longitudinally oblong sections; a single outstanding light band crossing the nape." The approximate distribution of whipsnakes that fit this concept of the subspecies *cingulum* is indicated by Stebbins (1966, map 132).

An examination of a large amount of material from Arizona and Sonora indicates a considerably more complex situation than was formerly recognized and requires a redefinition of this form. This new information reveals that *M. f. cingulum* is distributed from Moctezuma in eastern Sonora to, and including, Isla Tiburón to the west. It extends northward to intergrade with *M. f. picens* and *M. f. lineatulus* in Pima and Cochise counties in Arizona. It occurs at least as far south as the Sonora-Sinaloa border. The situation in northern Sinaloa is discussed in another section.

Masticophis flagellum cingulum exhibits more pattern variation than any other race of *flagellum*. This has been the primary reason for the confusion concerning *Masticophis flagellum* in Sonora. Bogert and Oliver (1945) discussed the problem in part. They stated that their material from Alamos and Guirocoba might be referable to any one of three subspecies, *picens*, *testaceus*, or *lineatulus*, and they noted that this being the case, "it becomes increasingly difficult to allot specimens from critical areas, and for the most part, identifications are not based on characters but on geographical data." Taylor (1936) and Zweifel and Norris (1955) noted the considerable variability of color pattern in the material they ex-

aminated, while continuing to use the name *piceus*.

I suggest the following explanation for this situation. *Masticophis flagellum cingulum* exhibits an unusual amount of variation in color pattern including a red phase (the phase originally described), a black phase (as in *M. f. piceus* and the Baja California form), a patternless phase (the phase discussed by Bogert and Oliver, 1945, p. 363, and thought to resemble *M. f. testaceus*), and intermediate patterns between these three phases. For purposes of discussion I have divided the wide spectrum of color pattern variation into seven pattern classes labelled as follows:

- A. Pattern of wide, dark red bands separated by light pink interspaces;
- B. As in A but with a reduced number of light bands;
- C. As in A but with only the nuchal band present;
- D. Uniform pink or tan dorsal coloration with no evidence of pattern;
- E. As in A but with a few black scales distributed on the anterior portion of the body;
- F. Anterior 1/3 to 1/2 of the body black, posterior 2/3 to 1/2 red;
- G. Solid black dorsal coloration.

The distribution of these color pattern classes is illustrated in Fig. 16. It will be noted that the individuals constituting the pattern A class tend to be concentrated in the northern and northeastern portions of the range. The patternless D class tends to be concentrated in southern Sonora, and the predominately black F and G classes are concentrated in central and western Sonora. The intermediate classes are rather indiscriminately distributed throughout the range.

Figure 16 only approximates the actual distribution. The phases A, D, F, and G tend to predominate and there are a lesser number of the intermediate phases B, C, and E. In the samples examined, the incidence of the seven color pattern classes is as follows: A—35.6%; B—5.9%; C—2.5%; D—12.7%; E—12.7%; F—23.7%; G—6.8%. Also, as mentioned above, classes A, D, F, and G tend to be concentrated in certain areas and also to predominate in those areas. In Santa Cruz County, Arizona, 84% are of pattern class A and 16% are of pat-

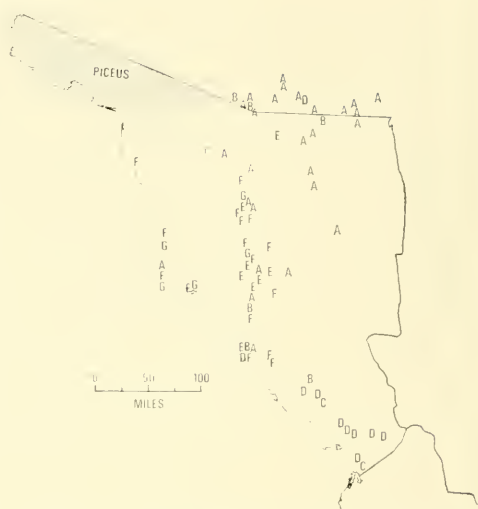


Figure 16. Distribution of the color pattern classes of *Masticophis flagellum cingulum* in Sonora.

tern class B. In Cochise County, Arizona, 89% are of pattern class A and 11% of pattern class D. From Naco, Sonora, south to Moctezuma, and west to Arizipe, 89% are of pattern class A and 11% of pattern class B. In the area from Imuris and Santa Ana south to Hermosillo, east to Mazatán and west to Pitiquito the following percentages obtain: A—18%, B—5%, C—3%, D—0%, E—26%, F—38%, G—10%. From Desemboque south along the coast to Empalme, including Isla Tiburón, the frequency of occurrence of the various pattern classes is as follows: A—8%, B—4%, C—0%, D—12%, E—15%, F—46%, G—15%. Finally, in the area between Ciudad Obregón, Alamos, and the Sonora-Sinaloa state border, 77% are of pattern class D, 15% are of pattern class C, and 8% are of pattern class B.

Thus, it may be seen that the percentage of pattern class A is highest in the region from Santa Cruz and Cochise counties south to Moctezuma (90% of the total number of pattern class A). Percentages of pattern classes F and G are highest in the area from Santa Ana and Imuris south to Hermosillo and west to Guaymas and Desemboque (100% of the total number of pattern F and G classes). Finally, percentages of pattern class D are highest in the area from Obregón south to the Sonora-Sinaloa border

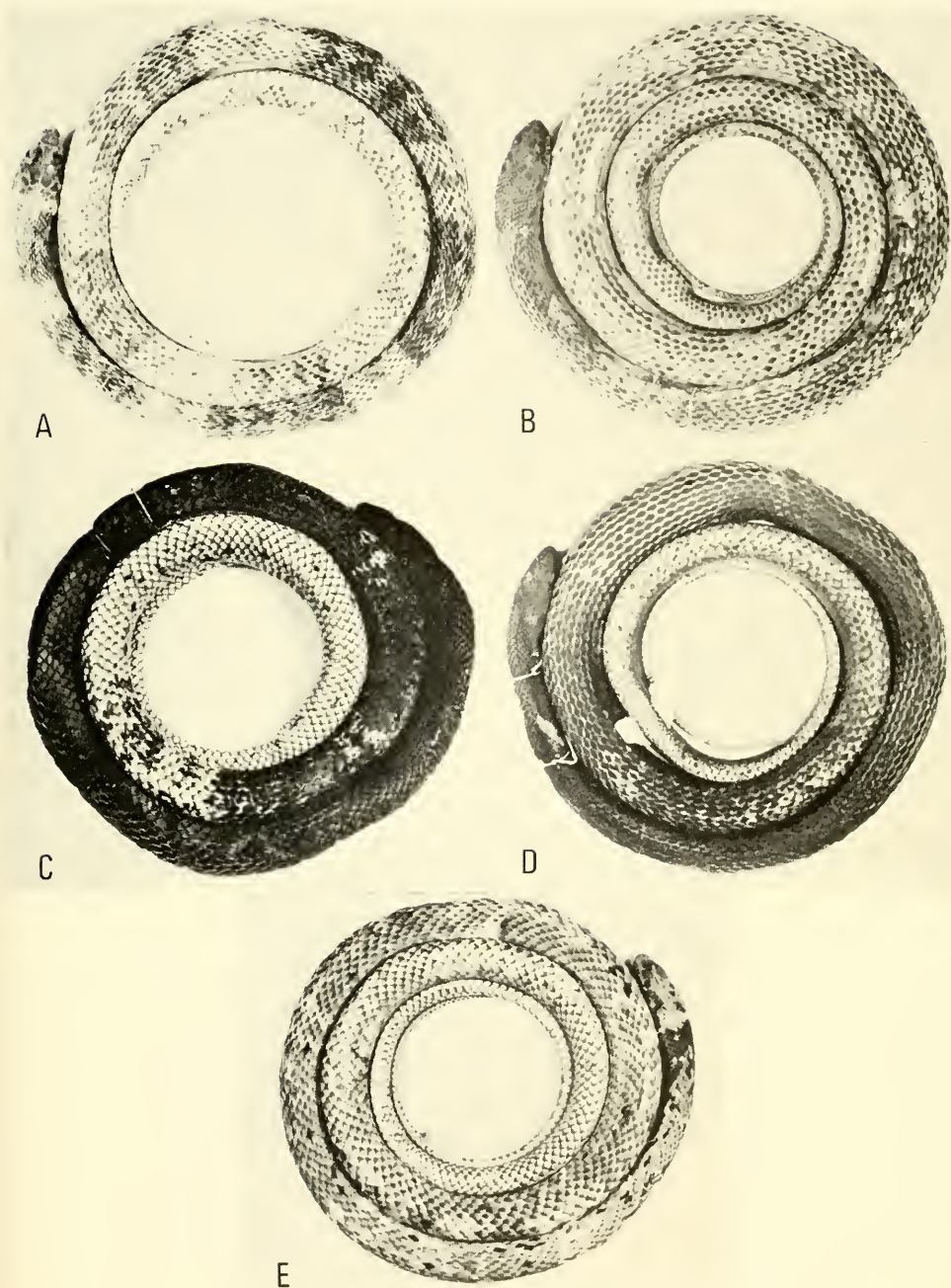


Figure 17. Pattern variation in *Masticophis flagellum cingulum*. A. *M. f. cingulum* (LSUMZ 10520) from Douglas, Cochise County, Arizona (Pattern A). B. *M. f. cingulum* (LACM 6996) from Terreros, Sinaloa, Mexico (Pattern D). C. *M. f. cingulum* (AMNH 99370) from 0.5 miles S San Miguel de Horcasitas, Sonora, Mexico (Pattern F). D. *M. f. cingulum* (LACM 25922) from 25 miles N Hermosillo, Sonora, Mexico (Pattern G). E. *M. f. cingulum* (KU 78957) from 7 kilometers W Kino, Sonora, Mexico.

(77% of the total number of pattern D class).

There is variability in each of the above color pattern classes and, in reality, there is a complete continuum from the A pattern to the D pattern and from the A pattern to the G pattern. The basic coloration of pattern A is given in the following description (based on color notes taken in life on LSUMZ 10520 from Douglas, Cochise County, Arizona; Fig. 17A). The dorsum has long, dark mahogany-red blotches separated by narrower interspaces that are composed of scales that are light at the base and dark brownish red at the tip. Within each light interspace is a band that is somewhat browner than the long bands. There are 10 or 11 dark red bands. These bands range from about 11 to 14 scales long. The light pink interspaces are 5 to 6 scales long and the dark band within these interspaces is about 2 scales long. Posteriorly, the long bands become less prominent and on the tail the color is like that of the interspaces on the more anterior portion of the body. Three scales behind the parietal there is a narrow (one scale long) band that is colored like the interspaces. The venter is dark pink with a slight orange cast. On the neck and forebody there is a double row of faint spots. The top of the head is dark red with the scales lightly outlined with white. The temporal scales are dark red. Most of the rostral is dirty white. The chin is white, blotched with tan and speckled with dark brown. The iris is golden orange and dark brown.

The long dark bands vary from 5 to 16 scales in length and the light interspaces from 2 to 6. The number of dark bands on the body varies from 9-12. Frequently there is a narrow light band in the center of the dark band and occasionally two of these are present.

I have seen no living material of pattern class B animals but the pattern, and probably the color, is similar to that of pattern class A animals except that the long bands are reduced in number.

Specimens that have a class C pattern are uniform pinkish tan, and the narrow light nuchal band is the only vestige of the class A pattern that remains.

I also have seen no living specimens of pattern class D, but Bogert and Oliver

(1945) described a specimen from Alamos as "uniform brownish olive above and essentially devoid of markings, although each of the lateral scales has a lighter area in the anterior median part. This specimen is similar in coloration to specimens of *Coluber flagellum testaceus* from Texas, although its coloration is somewhat darker than any specimens at hand. The sides of the head, including the lips are almost uniformly brownish and bear no trace of pattern found commonly on *piceus*." These authors did not state whether the color description was based on a living specimen. Joseph F. Copp has informed me (*in litt.*) that "the species [*Masticophis flagellum*] is also common on the same highway [Mexico 15] south of Navajoa where nearly uniformly red individuals seem to be the rule." Preserved specimens are uniform tan to light velvety brown without any trace of bands (Fig. 17B). The venter is cream with a double row of light-centered spots on the neck and forebody. The top and sides of the head are the same color as the dorsum of the body. The lower portion of the supralabials is cream and they are often blotched with dark brown. The chin is cream, mottled with brown.

The animals of pattern class D do, indeed, appear similar to some specimens of *Masticophis flagellum testaceus*, especially the pattern variety that is devoid of any dorsal markings. The most common pattern variant of *testaceus* is tan on the dorsum with narrow brown to dark brown bands on the neck, but the uniformly colored Sonoran specimens may be easily distinguished from this variety as well as from the wide-banded variety of *testaceus* discussed in the account of that subspecies. Separating nonpatterned *cingulum* and nonpatterned *testaceus* involves rather subtle distinctions, and, were it not for the fact that a continuum can be demonstrated from pattern A to D, it would be tempting to consider the convenient but zoogeographically untenable idea that nonpatterned *cingulum* are *testaceus*. The velvety appearance of the dorsal coloration in nonpatterned *cingulum* is something that I have not seen in *testaceus*. Also the dorsal color seems to be darker in *cingulum* than in *testaceus*. Any attempt to delineate these differences in a key would be fruitless, and identification should be made on the basis of geographic probability.

From the above it is obvious that a gradual obliteration of the banded pattern of class A animals occurs through classes B and C to pattern class D animals. This change is also indicated in the clinal shifting of the relative percentages of pattern A animals and pattern D animals from the northern portion of the range of *cingulum* to the southern portion. This same trend is also indicated to a lesser extent (due, perhaps, to lack of sufficient material) by the intermediate patterns B and C.

Pattern E animals exhibit considerable variation and grade almost imperceptibly from the typical A pattern to the F pattern. At one end of the spectrum are animals similar to pattern class A animals but with 3 or 4 dark scales on the neck and some dark markings on the side of the head (KU 48921, JFC 63-117). Others have a few more black scales on the neck (LACM 9136, 25166; AMNH 75129, 84979-80; UAZ 9336; KU 78957, 78959; see Fig. 17E). Others have aggregations of black or very dark brown scales on the neck (JFC 64-200) and farther posteriorly along the body (KU 78956, JFC 64-202, UIMNH 23917). This pattern type occurs primarily between Imuris and Guaymas.

Pattern F animals also exhibit variability in the amount of the body covered by black (Fig. 17C). This black coloration is present on about 1/3 to 3/4 of the anterior portion of the body. The remaining 2/3 to 1/4 of the body is colored with a variegated mixture of red and black that, in many specimens, takes a banded form. These bands are very similar, and in some specimens identical, to the bands of pattern A animals except that the dark red pigment is replaced by black. This type of banding is well evidenced in UNM 13705, MSU 7875, JFC 64-201, OSU 2029, and several uncatalogued specimens in the collection of the University of Arizona. More commonly, however, the black coloration is broken into long bands by lighter interspaces that are not bisected by a narrow black band. In these specimens the number of light bands varies from 2 to 7.

Pattern G animals are solid black dorsally (Fig. 17D), although certain specimens have some dark brown pigment on the posterior portion of the body. One specimen (LACM 25922; Fig. 17D), which is black

on the anterior 3/4 of the body grading to dark brown posteriorly with remnants of 3 lighter bands, is intermediate in coloration between those specimens that are classed as belonging to patterns F and G. The following description is of a living specimen of pattern class G (JFC 65-217). The dorsum is black except for the extreme tip of the tail which is blotched with pink. The venter is black on the anterior half of the body grading into pink on the posterior 1/4. The tail is dark pink ventrally. The head is very dark brown dorsally and laterally, except for a pink blotch on the loreal and upper preocular. The chin is very dark brown with fine white stippling on the anterior infralabials. The eye is golden orange around the pupil and dark brown around the edge.

The pattern described above is identical with the pattern exhibited by black *piceus* from the region of Tucson. The two forms do not come into contact, however, and each is connected, through a pattern gradient, with the more easily identified individuals of the subspecies *cingulum* and *piceus*. As is the case among the patternless phases of *cingulum* and *testaceus*, subspecific allocation must be made on the basis of geographic probability.

Masticophis flagellum fuliginosus (Cope),
new combination

Baja California Whipsnake

Bascanion flagelliforme testaceum: Yarrow, 1883: 112 (part)

Bascanion flagelliforme testaceum: Belding, 1887: 98

Bascanion laterale: Cope, 1890: 147

Zamenis lateralis fuliginosus Cope, 1895: 679

Bascanion flagellum frenatum: Van Denburgh, 1895: 148

Zamenis flagellum frenata: Mocquard, 1899: 323

Bascanion laterale fuliginosum: Van Denburgh, 1905: 26; Van Denburgh and Slevin, 1914: 145

Bascanion flagellum: Meek, 1906: 15 (part)

Coluber flagellum piceus: Van Denburgh and Slevin, 1921: 64; Schmidt, 1922: 683; Van Denburgh, 1922: 664 (part); Klauber, 1942: 88 (part)

Masticophis piceus: Ortenburger, 1928: 125 (part); Linsdale, 1932: 375

Masticophis flagellum frenatus: Ortenburger, 1928: 112

Masticophis flagellum frenatum: Linsdale, 1932: 375

Coluber flagellum frenatum: Mosauer, 1936: 16



Figure 18. Pale phase of *Masticophis flagellum fuliginosus* from 7 miles N San Pedro, Baja California del Sur, Mexico.

Masticophis flagellum piceus: Brattstrom and Warren, 1953: 179 (part); Cliff, 1954: 77; Murray, 1955: 45; Leviton and Banta, 1964: 150; Stebbins, 1966: 150 (part)

Syntypes.—USNM 15135-15136, collected on Santa Margarita Island, Baja California del Sur, Mexico, on 2 May 1888 by the crew of the U. S. Fish Commission vessel *Albatross*.

Diagnosis.—A subspecies of *Masticophis flagellum* with two color phases, one having a yellow or light gray dorsum with a zigzag pattern of black bands along the body and wider dark brown bands on the neck (Fig. 18), and the other having a dark grayish brown dorsum with a lineate pattern of variable length on the lateral portion of the dorsum, and a variable amount of cream coloration on the venter.

Range.—All of the peninsula of Baja California except for the portion east of the San Pedro Martir Mountains and north of Bahía San Felipe. The dark phase extends into the southern portion of San Diego County, California (Figs. 2 and 3).

Description of the Syntypes.—Scutellation (the first set of numbers applies to USNM 15135, the second to USNM 15136): supralabials 8-8, 8-8, the fourth and fifth entering the orbit in both; infralabials 10-10, 10-10, four touching the anterior chin shields and the fifth the largest in both; loreal 1-1, 1-1; preoculars 2-2, 2-2; postoculars 2-2, 2-2; temporals 8-8, 7-7; scale reduction pattern (of USNM 15135)

$$19 \frac{3+4(7)}{3+4(8)} \quad 17 \frac{3+4(108)}{3+4(112)}$$

$$15 \frac{\quad}{6+7(118)} \quad 14 \frac{\quad}{6+7(124)} \quad 13;$$

ventrals 192 (Cope gave an incorrect count of 201), 190 (Cope's count is 205); tail incomplete in both. Body lengths are 809 mm and 670 mm, respectively, tail incomplete in both.

Cope (1895) described the color pattern as follows: "Color above blackish-brown anteriorly, becoming lighter posteriorly to the end of the tail. The dark color extends on each end of the gastrosteges to the angulation throughout the length, and in the younger specimen [USNM 15136], fading out beyond the middle of the length. Ground color of belly yellow. In the larger specimen [USNM 15135] the black-brown predominates on the inferior surfaces, yielding gradually to the ground color, which predominates on the inferior surface of the tail. A yellow spot on the preocular; and in the younger specimen on the postoculars and labial plates. Gular and genial plates yellow spotted in the younger specimen, nearly uniform dark brown in the older. On the anterior part of the body of the younger specimen the lateral scales to the third and fourth row have brown shades, with an obscure trace of cross-banding. On the same specimen near the middle of the body, there are two pale half-cross-bands near together.

In the same, the center of each parietal plate is brown."

To this description I can add that both specimens show a light flecking throughout the length of the body and on the side of the neck, this being better developed in the smaller of the two specimens.

Discussion.—Meristic and mensural data for this subspecies based on 92 males and 70 females may be summarized as follows: supralabials 7 to 9, infralabials 8 to 11, preoculars 1 or 2, postoculars 1 to 3, loreal 1 or 2, ventrals in males 175 to 204, ventrals in females 176 to 205, subcaudals in males 100 to 129, subcaudals in females 99 to 123, dorsal scale rows 19-17-12 to 19-17-13. Body length in males of all ages ranges from 239 to 1320 mm, in females 237 to 1242 mm. Total length in males of all ages ranges from 317 to 1729 mm, in females 311 to 1676 mm. Tail length/total length ratios in males range from 0.209 to 0.288, in females 0.224 to 0.295.

Because of demonstrable and consistent differences in coloration and pattern, I recognize the populations of *Masticophis flagellum* inhabiting the greater part of the peninsula of Baja California as distinct, and, therefore, resurrect the name *fuliginosus* for this subspecies. The race was described by Cope (1895) from the Isla Santa Margarita, but he assigned it to the species *lateralis*. It was placed in the synonymy of *Coluber flagellum piceus* (= *Masticophis flagellum piceus*) by Schmidt (1922), who noted the resemblance of Cope's specimens to snakes from the mainland of Baja California. The name *Zamenis lateralis fuliginosus* has remained in the synonymy of *M. f. piceus* to this date.

This subspecies may be distinguished from *M. f. piceus* and all other races of *Masticophis flagellum* by the following characters: The dorsal coloration of the pale phase is some shade of yellow (usually bright yellow) or light gray (pink to red in *piceus*); the dorsal pattern consists of a series of transverse zig-zag bands, between which the ground color is uniformly pale (in *piceus* there is an alternating series of red and cream bands between the dark bands); and the dark bands in *fuliginosus* are formed by dark markings at the apex and anterolateral edges of each scale. Thus, since the scales of each dorsal scale row al-

ternate in position with those above and below, the placement of this pigment produces a zig-zag pattern.

The dark phase of *fuliginosus* may be distinguished from the dark phases of both *piceus* and *cingulum* by the following characters: The dorsal coloration is dark grayish brown; the scales of the anterolateral portion of the dorsum have pale lateral edges that give the impression of a pale, narrow line along the junction of each scale row with that above and below; this coloration extends for a variable length along the body; the head is usually brown, a little paler in coloration than the dorsum; a varying portion of the venter is cream to yellowish cream. In contrast, the dark phases of *cingulum* and *piceus* are solid black above and the posterior portion of the venter is salmon pink to salmon red; in these forms the head is the same color as the dorsum.

The following description of the color pattern of a specimen from Isla Carmen, Gulf of California (JFC 65-204), is characteristic of the pale phase of this subspecies. The greater part of the dorsum is yellowish tan. The ground color of the neck, however, is olive green and the scales are heavily speckled with black. There is an orange suffusion on the first dorsal scale row and to some extent on the second. The venter is pale yellow anteriorly and lemon yellow posteriorly. There is a double row of irregularly shaped cinammon blotches on the neck. The head is grayish brown dorsally. The lateral area of the head is similar with white blotches on the loreal, upper preocular, and supralabials. The chin is white with brown blotching.

The following description is of a dark phase *fuliginosus* from 21 to 22 miles S La Paz (LSUMZ 12630). The dorsum is dark brown grading to brown on the extreme posterior portion of the body and tail. The first dorsal scale row is a shade paler. The venter is dark brown on the throat grading to creamy white posteriorly. The head is dark brown above, brown laterally, with a white blotch on the sixth supralabial. The chin is brown with cream blotching, which extends to the posteroventral edge of the last supralabial.

Although there is some degree of variability in the intensity of the color pattern at any one stage in a snake's life, there is

a definite ontogenetic darkening of the pattern from juvenile to adult. This change is illustrated by the following description of a series of dark phase *fuliginosus* from various localities in Baja California del Norte in the collection of Mr. Joseph F. Copp.

New-born specimens have essentially the same color pattern as do the young of "red phase" *piceus*, but the color is much darker. There are dark brown bands on the neck separated by cream bars. The rest of the dorsum is covered with a mottling of dark and light brown. The venter is cream with dark brown spotting on the neck. The head is brown with cream blotching on the side. The chin is cream with brown mottling.

As a snake grows larger (as exemplified by JFC 441 from 2.2 miles S Colnett, Baja California del Norte, snout-vent length 472 mm) the entire dorsum begins to darken. The mottling is less evident and the pale interspaces between the neck bands are restricted to the side of the neck. Cream blotching on the side of the head is less extensive. The venter is much the same at this stage as in new-born animals.

At a snout-vent length of 967 mm (JFC 60-94 from 4.2 miles S Rosarito, Baja California del Norte), a snake is much darker. The dorsum is very dark brown from scale rows five or six to the middorsal row. Rows one to five or six have a lineate pattern that is more diffuse posteriorly. The cream interspaces on the neck are still visible although almost obscured by the lineate pattern. The venter is cream with a double row of light-centered brown spots. The head is darker and the brown blotching on the side of the head and chin is darker and more extensive.

As a snout-vent length of 1029 mm (JFC 60-100 from 2 miles N Arroyo San Telmo, Baja California del Norte) the dark coloration of the dorsum is more extensive, tending to obscure the lineate pattern on the side of the neck. Spotting on the venter is more prominent and the spots on the neck show indications of fusing together. The brown coloration on the side of the head and chin is more extensive.

At a snout-vent length of 1044 mm (JFC 398 from the San Telmo Valley, 3 miles E San Telmo, Baja California del Norte) the cream blotching on the side of the head has almost disappeared and the chin and

throat are heavily blotched with grayish brown.

At a snout-vent length of 1068 mm (JFC 59-73 from Punta Cabras, Baja California del Norte) the lineate pattern on the side of the neck has virtually vanished, and there is only a slight indication of it on scale row one.

At a snout-vent length of 1267 mm (JFC 60-110 from the north base of Punta Banda, Baja California del Norte) the side of the head and chin have very little cream blotching.

In summary, as a juvenile snake of the dark phase of *fuliginosus* attains adulthood, there is a progressive darkening of the dorsum, head, throat, and chin, and an intensification of the spotting on the venter.

The dorsum of the light phase of *fuliginosus* is either pale to dark yellow, pale tan to tan, or pale gray. Some specimens that have been long preserved are ivory-white in coloration; this may be the result of fading from an original pale gray coloration.

In a series of 14 specimens from Miraflores, 6 are yellow, 2 pale gray to grayish tan, and 6 are ivory-white. The number of specimens of each color type that I have examined from several localities in Baja California are as follows: La Paz—yellow (2), tan (1), pale gray to dark gray (3); Agua Caliente—yellow (1), tan (2); San José del Cabo—yellow (2), tan to grayish tan (3); Cabo San Lucas—yellow (3), tan (10), pale gray (2); Santa Anita—yellow (1), tan (3). That this difference in coloration is not due to variations in methods of preservation or storage of specimens is evident from the presence of both yellow and pale gray specimens in series collected at the same time. There is also variability in the amount of dark pigment on the body (Fig. 19).

Distribution of the dark and pale phases of the subspecies is shown in Figure 20, in which it is obvious that the black phase is more common in the northern portion of the peninsula. A single specimen of pale-phase *fuliginosus* (USNM 37551) is available from that portion of the peninsula. It was collected in Trinidad Valley at the northwest base of the San Pedro Mártir Mountains by Nelson and Goldman. On the other hand, the pale phase is the more abundant form in the southern part of the pe-

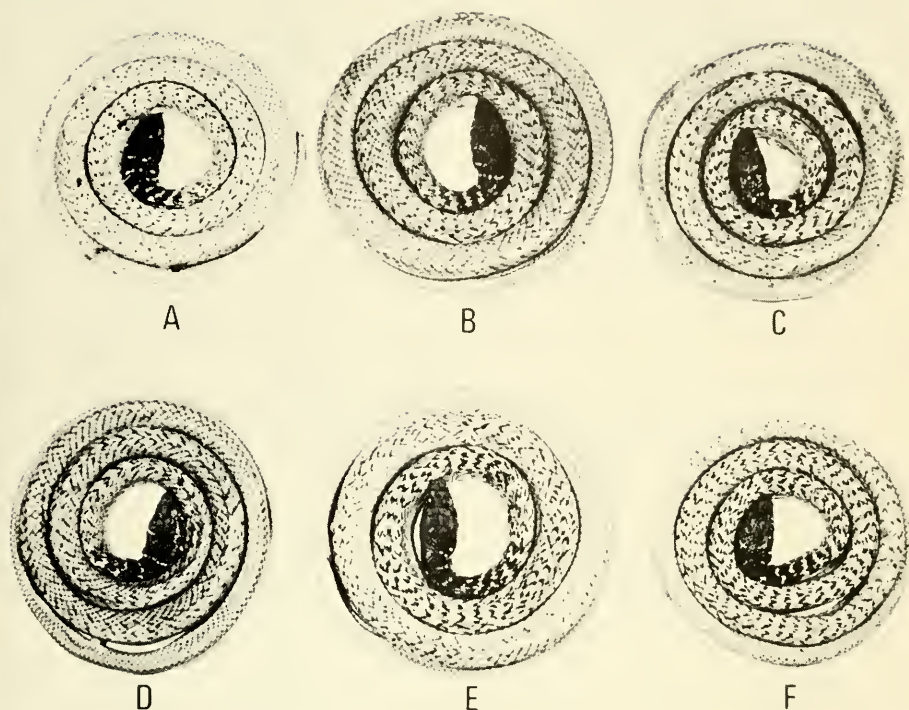


Figure 19. Dorsal view of six specimens of *Masticophis flagellum fuliginosus* showing the extent of variation in the amount of dark pigment in the dorsal pattern in the pale phase. The numbers for the specimens in the upper row, from left to right, are as follows: CAS 71150, 71151, 71147. For the bottom row, from left to right, the numbers for the specimens are as follows: CAS 71141, 71142, 71148. All specimens are from Cabo San Lucas, Baja California del Sur, Mexico.

ninsula. Of 81 adult specimens examined from Baja California del Sur, 66 are of the pale phase.

Only one phase has been found at most localities. There are, however, a few mainland localities where both have been collected. These localities, all in the southern part of the peninsula, are San Bartolo, San Pedro, Scammon's Lagoon, La Paz, San Antonio, and San Ignacio. Because the samples from each of these localities are small, it is useless to speculate which phase is more abundant in areas of sympatry.

Masticophis flagellum fuliginosus is known from many of the islands off both coasts of Baja California, but not from the islands adjacent to the northern portion of the peninsula. I have seen specimens from Isla

Magdalena and Isla Margarita (the type locality) on the Pacific side, and from Islas Coronados, Carmen, Monserrat, San José, Espíritu Santo, and Cerralvo in the Gulf of California. In addition this subspecies has been reported from Isla San Ildefonso (Klauber, 1942; Cliff, 1954).

Previously, each island was thought to be inhabited by only a single color phase (Klauber, 1942; Cliff, 1954). Whereas this is true of most of the islands, there are exceptions. Islas Carmen and San José have only the pale phase, and Islas San Ildefonso, Coronados, Espíritu Santo, Margarita, and Cerralvo have only the dark phase. Isla Monserrat has both phases, however, as does Isla Magdalena.

Though obviously related to the mainland

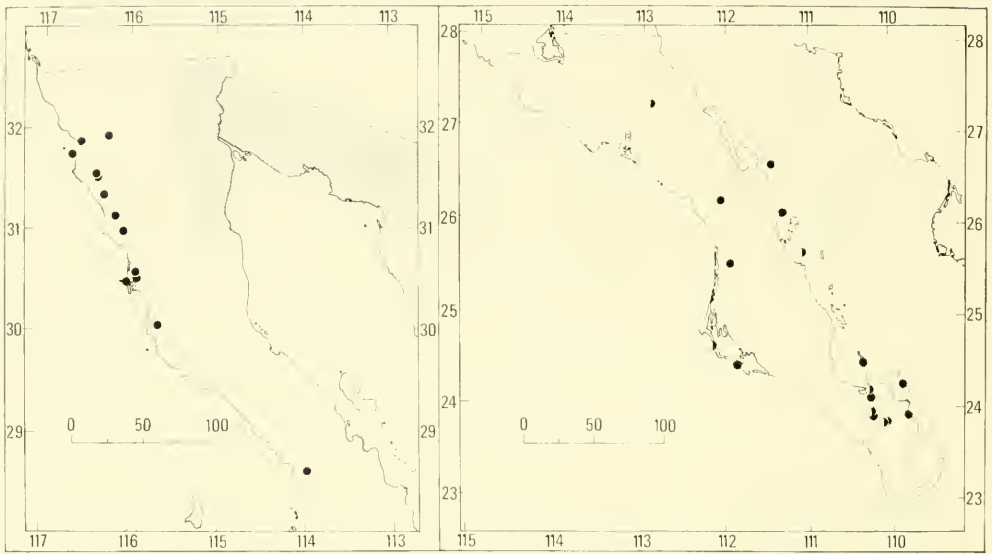


Figure 20. Distribution of the pale and dark phases of *Masticophis flagellum fuliginosus* in Baja California, Mexico. Black dots represent localities for the dark phase, open dots localities for the light phase, and half-filled dots localities for both. The stippled area indicates the range of *M. f. piccus*.

populations, the snakes from the islands show a considerable amount of interisland variation in color pattern (Figs. 21A and B). The population of dark phase snakes on Isla Coronados is very similar to the mainland populations. I have seen two specimens (SDSNH 30378, 30379) from this island. The larger of the two (snout-vent length 1309 mm) is very dark grayish brown on the anterior portion of the body, grading to dark brown posteriorly. There is some pale flecking laterally. The venter is largely cream (dorsal coloration extends onto the lateral edges of the ventrals) with a dark brown suffusion on the neck. The head is brown dorsally and laterally with cream spotting. The chin is cream with heavy brown blotching. The smaller specimen (snout-vent length 1112 mm) generally conforms to this description, but its dorsal

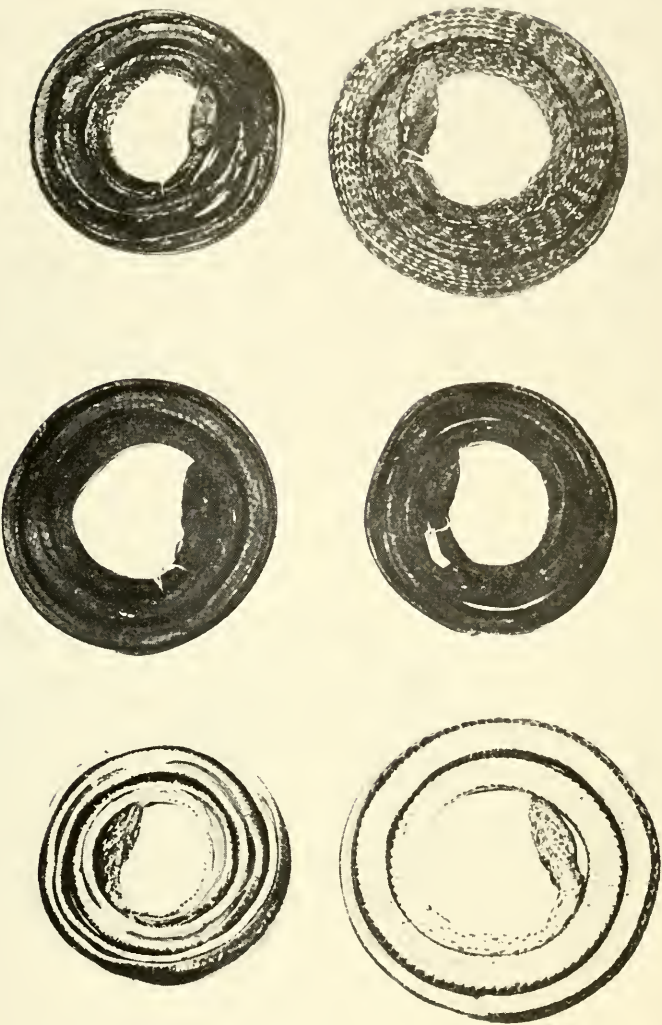
coloration is much paler. This description agrees well with the description given by Cliff (1954) for thirteen specimens from the same island.

The specimens I have seen from Isla Cerralvo (SDSNH 44373-74, 44481, 52708; UCM 26384-85; LACM 25070) are similar to one another in having the dorsum very dark brown, grading to dark brown posteriorly. The head is more or less uniformly dark brown dorsally and laterally. The venter is cream with the dark dorsal color extending onto it in patches, thus producing a checkerboard pattern. The lateral flecking is reduced or absent. Again there is agreement with the description given by Cliff (1954).

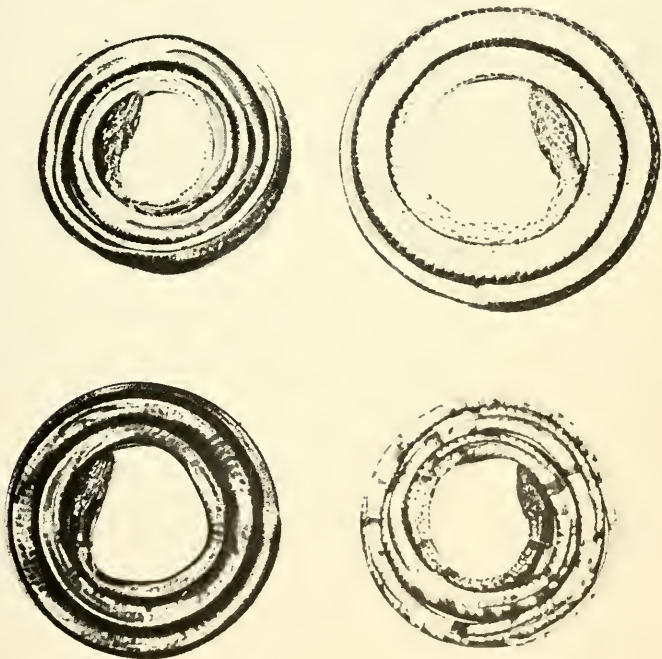
I have seen four specimens from Isla Espíritu Santo, three of which (SDSNH 44385, 3820, 44637) are similar to one

Figure 21. Interisland variation in the dark phase of *M. f. fuliginosus*. A. Dorsal view of four specimens from the islands in the Gulf of California. The numbers and localities for the specimens illustrated are as follows: upper left, SDSNH 30379, from Isla Coronados; upper right, SDSNH 44639, from Isla Monserrat; lower left, SDSNH 44637, from Isla Espíritu Santo; lower right, SDSNH 44373, from Isla Cerralvo. B. Ventral view of four specimens in the same order as in A.

A



B



another in color pattern. The other specimen (SDSNH 3821), however, resembles specimens from Monserrat. Although of different sizes, the first three specimens agree in having the total ventral surface heavily suffused with dark brown pigment. The largest specimen (SDSNH 44637) has a completely dark brown venter, except for some cream flecking in the region of the vent and along the midventral line of the tail. Dorsally this specimen is very dark brown with no lateral flecking except at the angle of the jaw. The smaller specimens show an intermediate stage in development of the adult pattern and are similar, except for the ventral coloration, to representatives of the mainland population. One specimen (SDSNH 3821) differs from the rest in having a cream venter which is only lightly suffused with dark brown pigment. It is identical to dark phase specimens from Monserrat, hence the locality data for this specimen may be in error.

The specimens of the dark phase from Monserrat (SDSNH 44375, 44480, 44639-40) are very dark grayish brown dorsally, grading to dark brown posteriorly. The venter is cream with a double row of brown spots on the neck and the forebody. They appear to differ from specimens from the other gulf islands in retaining dorsal flecking to a greater body length and in having the brown pigment of the venter more clearly arranged into a double row of spots. There is essential agreement with the description given by Cliff (1954) for specimens from Monserrat.

From Isla Santa Margarita I have seen only the two syntypes of *Zamenis lateralis fuliginosus*. They have been described above and they agree with the mainland population in color pattern. Two specimens (CAS 56048-49) examined by Klauber (1942), but not by me, are also of the dark phase.

Seven specimens have been examined from Isla Santa Magdalena (CAS 55887-91; SDSNH 3824, 10546). Both phases are present as well as specimens that are intermediate in coloration between the two (Fig. 22). The dark phase individuals agree well with those from the mainland. The dorsum is dark grayish brown with lateral flecking; the venter is creamy yellow with grayish brown spots on the neck and forebody, which break up into flecks posteriorly. One

specimen (CAS 55890) is intermediate in coloration. It has a snout-vent length of 1440 mm but is much paler than CAS 55888, which has a snout-vent length of 1365 mm.

The pale whipsnakes I have seen from the islands all have a yellowish ground color. The animals from Isla San José (UCM 26137; SDSNH 6872, 44638, 44641-43) and Isla Carmen (JFC 65-204, UCM 27269-70, SDSNH 3824) are more or less similar to one another and to the pale phase snakes from the mainland. A single specimen (SDSNH 44375) from Isla Monserrat is much more heavily speckled with dark pigment dorsally than are those from San José and Carmen. A pale phase snake from Isla Magdalena (SDSNH 10546) is also similar to animals from the above-mentioned islands and to the animals from the mainland.

In summary, specimens of *M. f. fuliginosus* from the islands off both coasts of Baja California del Sur show varying degrees of affinity to the snakes of the mainland populations and tend to be more stable in color pattern than those from mainland populations. Consistent interisland differences in color pattern appear to have become established. There is more color pattern variability in the dark phase than in the pale phase snakes. The level of divergence of color pattern between the island snakes, especially those of the gulf islands, and the mainland snakes might prompt some workers to describe new subspecies. It appears to me, however, that this would only obscure the situation by de-emphasizing the close relationships of the island populations to those of the mainland, with which their affinities obviously lie.

Dark specimens are also known from San Diego County, California. I have examined specimens of the pale phase from San Diego County that either were red (if freshly preserved) or, probably, would have been red in life. This information corroborates Klauber's statement that San Diego County specimens are predominantly red. They also agree in general pattern with snakes of this phase found farther north and east, and I have no hesitation in referring them to the subspecies *piceus*. On the other hand, the San Diego County specimens of black phase *fuliginosus* that I have examined (SDSNH 2144, 7579, 13710,

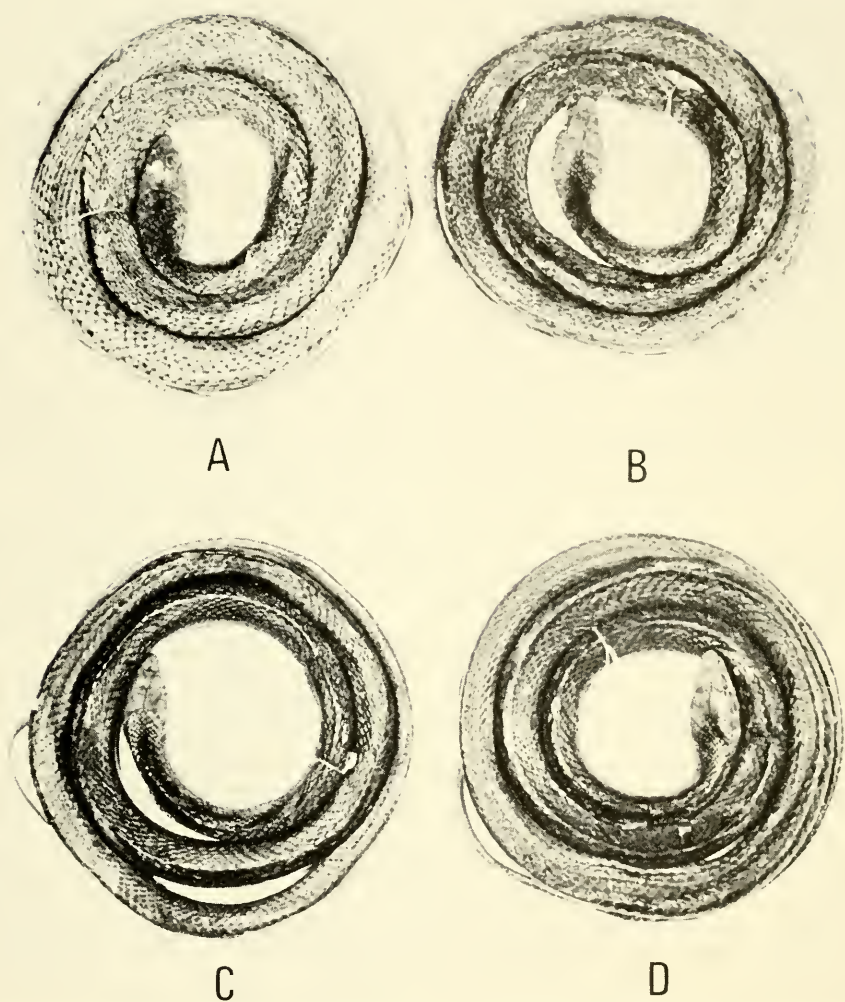


Figure 22. Dorsal view of four specimens of *Masticophis flagellum fuliginosus* from Isla Santa Magdalena, Baja California del Sur, Mexico. The numbers for the specimens illustrated are as follows: (A) CAS 55890; (B) CAS 55889; (C) CAS 55887; (D) CAS 55888.

25600, 44341) agree in every respect with black *fuliginosus* from farther south in the peninsula of Baja California and are distinct from black *piceus*. It appears that the red phase of *piceus* and the black phase of *fuliginosus* are not sympatric within San Diego County; *fuliginosus* occurs in the extreme southern portion of the county and *piceus* occurs in other areas. I have seen no intermediate specimens but such are to be

expected in areas of contact. Interpretation of intergradation between these two subspecies may be difficult inasmuch as it is the pale phase of *piceus* and the dark phase of *fuliginosus* that occur in San Diego County.

Populations of Questionable Status

There remains a problem regarding the status of the populations of *Masticophis*



Figure 23. Dorsal view of a specimen of *Masticophis flagellum* from El Dorado, Sinaloa, Mexico (AMNH 90730).

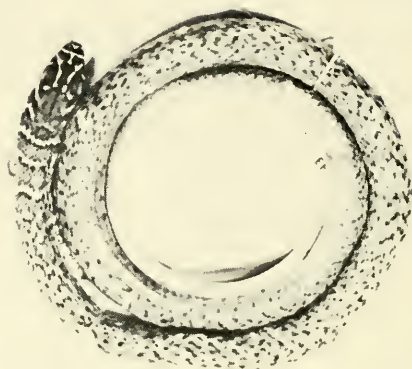


Figure 24. Dorsal view of a juvenile specimen of *Masticophis flagellum* from Hacienda Simón, 7.6 miles N Culiacán, Sinaloa, Mexico (UMMZ 120233).

flagellum in northern Sinaloa. I had been under the impression that the specimens from this area were all of the pattern D type of *M. f. cingulum*, i.e., unicolorous. However, during the final stages of this study I received several specimens that did not fit my concept of *cingulum*. This material includes individuals of all size groups.

As previously noted, southern populations of *cingulum* lack the banded pattern that is typical farther north, and adults are uniformly tan or brown dorsum (in preserved material). I have seen no living specimens from southern Sonora, but Joseph F. Copp has reported that specimens from the area are nearly uniform red.

In Sinaloa the large adults are nearly uniform tan in color (in preservative), but have some small gray or black spots on many of the dorsal scales (LACM 6995-96). Subadult specimens (AMNH 90728-32; KU 67688) usually have more pronounced spotting and, in addition, they retain the typical juvenile head pattern of the *piceus* group until they attain a greater body size than is the case in either *cingulum* or *piceus* (Fig. 23). The dorsal head pattern is much more pronounced than in juvenile *cingulum*. The border of each dorsal head scale is outlined with white or cream. The area immediately within the cream area is dark brown and the middle portion of the scale is pale

brown. The juveniles, although they have the typical *piceus* group juvenile pattern, have brighter head markings and a more spotted dorsum.

The following description is of the head pattern of UMMZ 120233, a juvenile from Hacienda Simón, 7.6 miles N Culiacán, Sinaloa (Fig. 24). The internasals and prefrontals have wide cream borders anteriorly and medially. The greater part of each scale is dark brown; the posterior edge is tan. The frontal is edged with cream anteriorly and tan laterally. Inside this area there is another narrow region of dark brown. The middle of the frontal is pale brown. The supraoculars are edged with cream anteriorly and laterally and tan posteriorly. Most of the rest of the scale is dark brown except for the median and outer lateral portions, which are light brown. The parietals have a cream spot anteriorly and a continuation of the cream stripe on the upper postocular onto the anterolateral area. The lateral edge of the parietal is edged with dark brown. The ventral portion of the rostral is cream. The upper half is brown with a central light brown blotch. The anterior nasal is mostly brown except for the anterior edge, which is cream. The posterior nasal is dark brown dorsally and ventrally with a central cream area. The loreal is dark brown with an anteromedial cream blotch.

The upper preocular is dark brown along, and dorsal to, the canthus rostralis; the ventral portion is cream. The lower preocular is cream anteriorly, dark brown posteriorly. The upper postocular is dark brown with a central cream stripe. The supralabials are cream with dark brown blotching. The temporals are cream with dark brown blotching.

These specimens differ from *M. f. cingulum* in having, as adults, a patternless dorsum, except for some small spots on the dorsal scales, and in having the juvenile head pattern accentuated and retained in larger individuals. Subadult specimens from Sinaloa are patternless, whereas adult *piceus* are banded. In addition, juveniles from Sinaloa are much more brightly marked than juvenile *piceus* and the dorsum is more spotted.

These specimens from Sinaloa may represent a distinct pattern form that deserves subspecific recognition. I have seen insufficient material, however, to make such a decision at this time.

KEY TO THE SUBSPECIES OF ADULT

Masticophis flagellum

This key is designed so that all pattern phases of the subspecies of *Masticophis flagellum* may be identified.

1. Each dorsal scale (at least on the anterior portion of the body) with a dark brown to black medial line; mid-portion of venter bright yellow; subcaudals and posterior portion of venter with a salmon pink to red posterior border which does not fade in preservative *Masticophis flagellum lineatulus*
Pattern not as above 2
2. Anterior 1/3 to 1/2 of dorsum dark to very dark brown (some specimens nearly black), posterior 2/3 to 1/2 brown to tan (in black specimens, the posterior portion of the venter and underside of tail are cream as opposed to the pink coloration (in life) of this area in black *M. f. piceus* and *M. f. cingulum*)
Masticophis flagellum flagellum
Color pattern not as above 3
3. Some portion of dorsum red or pink in life (tan or light brown in preservative)
Dorsum not red or pink 10
4. Anterior portion of dorsum solid black, posterior portion red 5
Pattern not as above 6
5. Posterior 1/3 to 1/2 of body with a pattern of black bands separated by

light red (tan in preservative) interspaces; sometimes a narrower, black band bisects the light interspaces

Masticophis flagellum cingulum
(pattern F)

Posterior 1/3 to 1/2 of body with a variegated pattern of red and black scales with no division into dark bands and narrow, light interspaces

Masticophis flagellum piceus
(intermediate phase)

6. Dorsum dark red to dark reddish-brown, this coloration being broken into long bands (11 to 14 scales long) by light (pink in life) interspaces 5 to 6 scales in length. A dark narrow band usually bisects each light interspace. This type of pattern usually extends the length of the body (pattern class A) but some specimens have this banding reduced and confined to a variable amount of the anterior portion of the body (pattern class B) 7
Dorsal banding, if present, confined to neck 8
7. Some black scales on neck
Masticophis flagellum cingulum
(pattern type E)
No black scales on neck
Masticophis flagellum cingulum
(pattern classes A and B)
8. A single light band across nape
Masticophis flagellum cingulum
(pattern C)
Pattern not as above 9
9. Dorsum with relatively long (3 to 4 scales long) black, gray, or brown (also sometimes the same color as the dorsum, outlined anteriorly and posteriorly with darkened pigment) bands on neck and a light, dark-bordered stripe through loreal
Masticophis flagellum piceus
(red phase)
Dorsum uniformly pink or salmon pink with slight banding on neck (bands, when present, narrow, about 1 scale long); no light, dark-bordered stripe through loreal
Masticophis flagellum testaceus
(pink phase)
10. Dorsum tan to light brown, yellow or light gray, or light yellow to light olive yellow 11
Dorsum dark grayish-brown to black 17
11. Dorsum tan to light brown 12
Dorsum yellow, light gray, or light yellow to light olive yellow 16
12. Remnants of juvenile pattern present; dark juvenile head markings of *flagellum* group present on dorsal head scales; bands on neck dark brown and well defined
Masticophis flagellum flagellum
(pale phase)
Dorsal pattern not as above 13
13. Dorsum uniform tan to light brown (at least in preservative) with no pattern

- Masticophis flagellum testaceus* (patternless phase), *Masticophis flagellum cingulum* (patternless phase), and Sinaloan specimens
Dorsum tan with some type of pattern 14
14. Dorsum uniform tan to light brown with a narrow, light band across nape of neck ... *Masticophis flagellum cingulum* (pattern C)
Dorsal pattern not as above 15
15. Dorsum with narrow (usually 1 and sometimes 2 scales long) brown to dark brown bands on neck and forebody; dorsum of head more or less uniform in coloration
..... *Masticophis flagellum testaceus* (narrow-banded phase)
Dorsum tan with wide, brown bands separated by narrower, lighter interspaces; wide bands sometimes composed of a series of dark brown narrow bands which are separated by a much lighter, shorter series of narrow bands
..... *Masticophis flagellum testaceus* (wide-banded phase)
16. Dorsum yellow or light gray with narrow, zig-zag black bands on dorsum, and with wider dark brown bands on neck; a double row of brown to dark brown spots on anterior portion of venter
..... *Masticophis flagellum fuliginosus* (pale phase)
Dorsum light yellow to light olive yellow; pattern absent or with obsolete bands on neck more or less the same color as the ground color; no spotting on anterior portion of venter
..... *Masticophis flagellum ruddocki*
17. Dorsum and head completely black; posterior portion of venter and underside of tail salmon pink to red
..... *Masticophis flagellum piceus* (black phase) and *Masticophis flagellum cingulum* (black phase)
Dorsum dark grayish-brown with indication of light lines on a variable amount of the lateral area of the dorsal scales; head usually somewhat lighter than rest of dorsum; venter usually completely cream with a double row of dark spots on anterior portion (specimens with a variable amount of dark pigment on anterior portion of venter still have cream coloration on posterior portion of the body) *Masticophis flagellum fuliginosus* (dark phase)

SIGNIFICANCE AND EVOLUTION OF COLOR PATTERN

Masticophis flagellum is one of the most variable snakes in North America. Not only is the species divisible into geographic races, but almost all the subspecies exhibit pattern

variations. Only two, *M. f. lineatulus* and *M. f. ruddocki*, do not. Also, most of the subspecies exhibit an ontogenetic change in color pattern. Only *M. f. testaceus*, of the *testaceus* group, and the red phase of *M. f. piceus* and the pale phase of *M. f. fuliginosus*, both of the *piceus* group, show very little change in color pattern from juvenile to adult.

The types of variation in adult pattern within the subspecies of *Masticophis flagellum* fall into four categories. These are: (1) clinal variation, (2) random variation, (3) non-clinal geographic variation, and (4) polymorphic variation. Clinal variation in color pattern is exhibited by *M. f. flagellum* and *M. f. cingulum*. In *M. f. flagellum* the color pattern is paler (has less dark brown pigment on the anterior portion of the body) in the southeastern portion of its range and is darker in the northwestern portion of its range. In *M. f. cingulum* there are two, more or less parallel clines within the range. First, there is a clinal trend toward loss of the banded pattern (pattern A), found most commonly in the northern and northeastern portions of the range, to the unicolor pattern (pattern D), found most commonly in the southern portion of the range. Second, there is another clinal trend toward progressive melanization of the banded pattern (pattern A) of the northern and northeastern portion of the range to produce the black pattern (pattern G), found in the central and eastern portions of the range. This deposition of black pigment takes place from anterior to posterior, and some specimens are totally black dorsally, thus paralleling the type of pattern seen in the black phase of *M. f. piceus*.

Random variation is seen in all subspecies, but it is most conspicuous in *M. f. testaceus*, in which the variation in color pattern is discontinuous, *i.e.*, there are three distinct patterns found in varying proportions throughout the range.

Geographic variation within subspecies limits is seen in *M. f. flagellum* and *M. f. testaceus*. In *M. f. flagellum* there is a pale tan phase centered in Florida, the adult pattern of which closely resembles the pattern of all juveniles of the *testaceus* group generally, and the pattern of juvenile *flagellum* particularly. This phase has a clearly defined, albeit discontinuous, range in portions

of Florida and Georgia (a single comparable specimen from North Carolina was also seen). In *M. f. testaceus* there is a pink phase, which differs from the more common and widespread tan form. This phase inhabits three disjunct areas in Trans-Pecos Texas, eastern New Mexico, and eastern Colorado.

Polymorphism is seen in *M. f. piceus* and *M. f. fuliginosus*. Both subspecies have a pale (red in *piceus*, yellow, tan, or light gray in *fuliginosus*) and a dark phase (black in *piceus*, dark grayish-brown in *fuliginosus*). Intermediate specimens are more common in the case of *piceus*, less so in *fuliginosus*. There is a dearth of information on the basis for this polymorphism. It is not known whether dark phase adults always give birth to dark phase young and light phase adults to light phase young, or whether both might appear in a single brood of either phase as is the case in *Lampropeltis getulus californiae* (Klauber, 1944). There is no information, other than that which I have presented in discussing color pattern variation, on the relative frequency of each color pattern in any given population. It is known that the range of the black phase of *M. f. piceus* is centered around Tucson, and that radiating from that central point the phase becomes less frequent in occurrence. It is also known that within its range the black phase is most common, the intermediate phase next, and the pale phase least common.

Within the subspecies *fuliginosus* the picture is less clear, largely because of insufficient material. Are there areas where only the pale phase occurs, as is suggested by the specimens available from the extreme southern cape region of the peninsula of Baja California and some of the gulf islands? Are there areas where only the dark phase occurs, as is suggested by material from the northwest coast of Baja California del Norte and others of the gulf islands? If so, why is this the case and why is it that both phases occur in some areas? What is the genetic basis of this pattern dimorphism? It would appear that neither in the case of *piceus* nor that of *fuliginosus* is it based on a single pair of alleles, for intermediate specimens do exist, which suggest the action of modifier genes in producing the adult pattern. Mayr (1963, p. 151)

stated "the genes involved in polymorphism have, in general, conspicuous discontinuous effects, and different genotypes (except some heterozygotes) can be distinguished phenotypically." If the intermediate is considered a heterozygote, resulting from the crossing of a homozygous pale phase snake with a homozygous black phase snake, then the situation cannot be designated as balanced polymorphism, which is maintained by "overdominance" of the heterozygote (Mayr, 1963, p. 221). In fact, the intermediates appear with a much lower frequency than either the pure dark or pale phases, at least in the peninsula of Baja California. Thus the usual solution to the problem of the maintenance of polymorphism does not seem to apply here.

This situation is similar to that described for the screech owl (*Otus asio*) by Owen (1963). Two phases of the screech owl, a gray one and a rufous one, exist over the portion of eastern United States lying east of meridian 104° W. Intermediate specimens also occur, as is the case among the whip snakes. The relative frequency of rufous screech owls varies geographically, as does the relative frequency of intermediate birds. Owen suggested that this type of polymorphism, which he preferred to call bimodal variation, is the result of a balance of selective forces acting on each phase and that the presence and maintenance of these two phases "represent balanced adaptations of the forms to varying environmental conditions." He goes on to say that "the existence of two distinct forms with few intermediates throughout much of the range of the screech owl in eastern North America is indicative of selection for bimodal variation. In most areas, selection must be continually operating against intermediates, but in Florida, where intermediates are frequent . . . , there is presumably a relaxation of selection pressure. The result of this is that while all six color categories [a pattern classification used by Owen to determine the frequencies of intermediates] occur in Florida, the population is extremely variable, but not polymorphic. Hence in the screech owl the unusual situation exists in which polymorphism for color and pattern is maintained over a large geographical area (eastern North America), while in a much smaller area (Florida) the complete range

of phenotypes occur, but the population is not polymorphic." West of the 104th meridian all the birds are gray.

Although the characteristics of the polymorphism exhibited by the subspecies *piceus* and *fuliginosus* are less well documented, there appear to be some differences from the review presented by Owen for the screech owl. Some of these are due to the smaller range inhabited by the black phase whipsnakes and to the smaller number of specimens available for study. In *fuliginosus*, however, it appears that intermediates are few in number, thus presenting a condition approaching bimodal variation. In *piceus*, on the other hand, intermediate specimens are of rather frequent occurrence and there would seem to be little selective pressures acting against the maintenance of this type of pattern. Also, in the area where the black phase of *piceus* occurs, it is the most common phase, and the light phase is the least common. Thus, at least in the case of *piceus*, there would appear to be little selection for bimodal variation.

In any event, to place a name on the type of variation exhibited by *piceus* and *fuliginosus* would be no solution to the problem of why, in certain areas, a polymorphic phase is maintained. If there are subtle differences in niche preference, it is not presently known what they might be. There is, in fact, very little information on any aspect of the ecology of *Masticophis flagellum*.

It is evident from a study of juvenile pattern, that there are two main evolutionary lines within the species *flagellum*. One, an eastern group of three subspecies (*flagellum*, *testaceus*, and *lineatulus*), is characterized by having a juvenile pattern composed of a tan dorsum with narrow, dark crossbands (usually 1 scale long, sometimes 2) separated by wider interspaces (Fig. 25). The other, a western group of four subspecies (*piceus*, *cingulum*, *ruddocki*, and *fuliginosus*), differs from the eastern group in having relatively long neck bands (3 to 4 scales in length) and narrow (1 scale in length) interspaces (Fig. 25). The members of this western group also have a pale streak through the nasal and loreal scales. This streak usually is straight-edged and longitudinal, and usually extends completely through the loreal, joining with

a pale blotch on the upper preocular. In contrast, in the eastern group, the pale spots on the nasal and loreal scales are not in contact but are separated by a thin stripe of brown pigment along the posterior edge of the posterior nasal. Also, the pale spots on the nasal and loreal are not oriented longitudinally, and the spot on the loreal is not in contact with the spot on the upper preocular. There is considerable irregular cream blotching on the temporals of the western group, which is less evident or absent in the eastern group.

In both groups there is a subspecies that retains the juvenile pattern essentially unchanged to the adult stage. In the eastern (*testaceus*) group it is the subspecies *testaceus*, and in the western (*piceus*) group it is the subspecies *piceus*. The other subspecies of each group have departed in varying degrees from this pattern, at least in the adult color pattern.

Thus, the division of the species *flagellum* into two stocks appears to have taken place at an early time, inasmuch as the basic patterns of the *piceus* and *testaceus* groups are markedly different. None of the juvenile patterns of the subspecies in either group shows any approach in basic pattern to juveniles of the subspecies of the other group.

Within the *testaceus* group, the subspecies *testaceus* is the central form from which the other two subspecies, *flagellum* and *lineatulus*, have diverged. *M. f. flagellum* has invaded the eastern United States and become adapted to the Austroriparian type of vegetation. *M. f. lineatulus* has invaded the Chihuahuan Desert of the northern portion of the Mexican Plateau. These two subspecies have diverged from more or less opposite ends of the range of the *testaceus*-like ancestor and have little in common with each other, *flagellum* having developed a dark brown anterior body color and *lineatulus* a lineate dorsum and a salmon-red venter.

Within the *piceus* group the subspecies *piceus*, or its ancestor, is the central stock from which the other subspecies have diverged. One subspecies has invaded Mexico west of the Sierra Madre Occidental and evolved a different type of banded pattern from that seen in *piceus*. This is the subspecies *cingulum*. The subspecies *ruddocki*

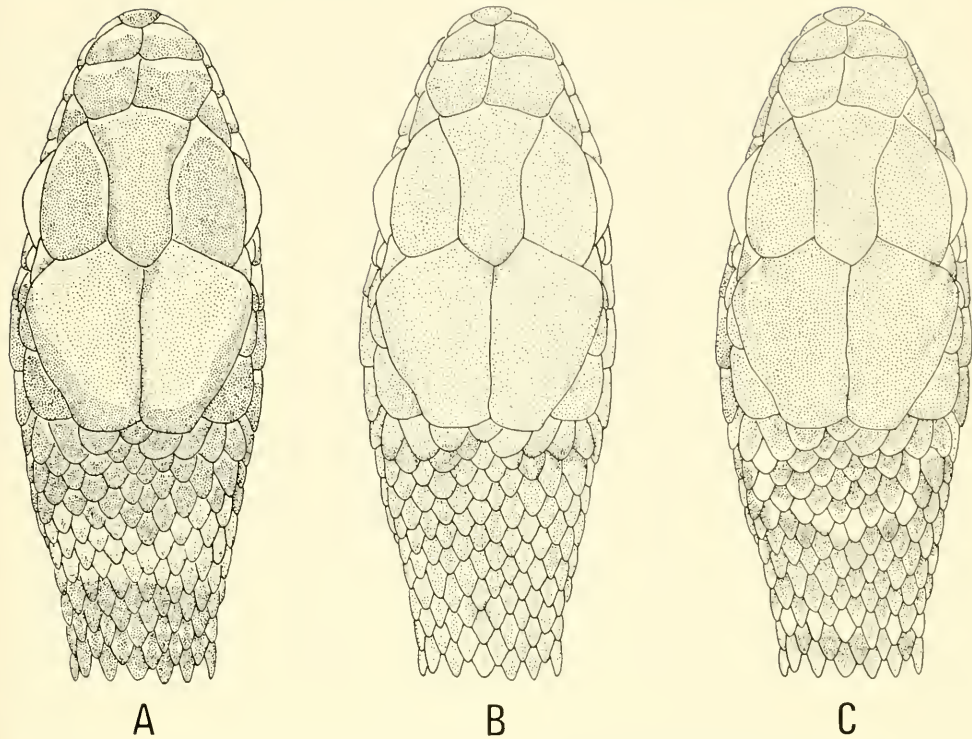


Figure 25. Dorsal view of the head of juvenile *Masticophis flagellum flagellum* (A), *M. f. tescatus* (B), and *M. f. piceus* (C).

has invaded the central valley of California and developed a pattern lacking the type of neck banding seen in *piceus* and having a different ground color. The subspecies *fuliginosus* has invaded the peninsula of Baja California and developed a basically different ground color and a slightly different type of banding on the dorsum.

VARIATION IN SCUTELLATION
AND PROPORTIONS
Head Scutellation

Supralabials.—The number of supralabials is normally 8, the fourth and fifth entering the orbit. Variation from this number is infrequent. Only 7.9% of the specimens examined has a count other than 8-8. Departures from the usual 8-8 condition involve the fusion or division of scales. Increase in the number of supralabials most often involves the division of the third supralabial (82.1%), but may also involve the division of the fourth (10.7%), second

(3.6%), eighth (2.4%), or fifth (1.2%). Decrease in the number of supralabials most often involves the fusion of the second and third supralabials (52.0%), but may also involve the fusion of the seventh and eighth (36.0%), or the fourth and fifth (12.0%). One specimen (TNHC 29117) has the second and third supralabials fused and the seventh divided giving the normal count of eight. The third and seventh supralabials are divided in JFC 63-150. In TNHC 7341 only the fifth supralabial enters the orbit. What apparently has taken place is that one of the anteocular supralabials is divided (probably the third) and the fourth and fifth are fused. In UCM 31533 the fourth supralabial does not enter the eye on the left side and is not present on the right. NTSU 193 has the seventh supralabial fused with one of the temporals. Variation in these scales is shown in Tables 4 and 5.

Infralabials.—The number of infralabials is most often 10 on each side of the head

TABLE 4.
Variation in number of supralabials in *Masticophis flagellum*.

Subspecies	7-7	7-8	8-8	8-9	9-9	Total
<i>flagellum</i>	—	3	321	16	2	342
<i>testaceus</i>	4	10	499	27	5	545
<i>lineatulus</i>	—	—	29	4	1	34
<i>piceus</i>	—	1	238	12	—	251
<i>cingulum</i>	—	1	74	2	1	78
<i>ruddocki</i>	—	—	9	3	—	12
<i>fuliginosus</i>	2	2	49	9	—	62
TOTAL	6	17	1219	73	9	1324

TABLE 5.
Variation in number of supralabials entering orbit in *Masticophis flagellum*.

Subspecies	3+4	3+4	4+5	4+5	5+6	4	5	4	Total
	3+4	4+5	4+5	5+6	5+6	4+5	5	4	
<i>flagellum</i>	—	3	321	16	2	—	—	—	342
<i>testaceus</i>	1	5	491	27	3	2	2	1	532
<i>lineatulus</i>	—	—	29	4	1	—	—	—	34
<i>piceus</i>	—	1	238	11	—	—	—	—	250
<i>cingulum</i>	—	—	75	4	1	—	—	—	80
<i>ruddocki</i>	—	—	9	3	1	—	—	—	13
<i>fuliginosus</i>	1	3	50	9	—	—	—	—	63
TOTAL	2	11	1213	74	8	2	2	1	1313

TABLE 6.
Variation in number of infralabials in *Masticophis flagellum*.

Subspecies	8-10	9-9	9-10	9-11	10-10	10-11	10-12	11-11	11-12	12-12	11-13	8-9	8-11	Total
<i>flagellum</i>	1	2	22	1	159	80	8	35	8	1	1	—	—	318
<i>testaceus</i>	1	17	54	8	248	121	3	29	6	1	—	1	1	490
<i>lineatulus</i>	—	—	6	1	14	5	1	—	—	—	—	—	—	27
<i>piceus</i>	—	1	12	4	101	74	5	39	5	—	—	—	—	241
<i>cingulum</i>	—	—	4	—	31	20	3	11	2	—	—	—	—	71
<i>ruddocki</i>	—	—	1	—	3	3	1	2	—	—	—	—	—	10
<i>fuliginosus</i>	—	6	8	—	36	9	—	2	—	—	—	1	—	62
TOTAL	2	26	107	14	592	312	21	118	21	2	1	2	1	1219

TABLE 7.
Variation in number of infralabials contacting anterior chin shields in *Masticophis flagellum*.

Subspecies	3-3	3-4	4-4	4-5	5-5	Total
<i>flagellum</i>	1	—	283	26	4	314
<i>testaceus</i>	—	4	460	17	1	482
<i>lineatulus</i>	—	—	23	3	1	27
<i>piceus</i>	1	—	230	8	2	241
<i>cingulum</i>	—	1	68	3	—	73
<i>ruddocki</i>	—	—	6	6	—	12
<i>fuliginosus</i>	7	2	53	—	—	72
TOTAL	9	7	1123	63	8	1210

TABLE 8.
Variation in number of loreals in *Masticophis flagellum*.

Subspecies	0-1	1-1	1-2	2-2	2-3	Total
<i>flagellum</i>	3	341	3	5	1	353
<i>testaceus</i>	—	515	15	4	—	534
<i>lineatulus</i>	1	32	—	—	1	34
<i>piceus</i>	—	253	1	—	—	254
<i>cingulum</i>	1	78	—	—	—	79
<i>ruddocki</i>	1	11	—	—	—	12
<i>fuliginosus</i>	—	69	1	—	—	70
TOTAL	6	1399	20	9	2	1436

(48.6%), 4 infralabials being in contact with the anterior chin shields, the fifth the largest. Deviations from this number, however, are manifold (Tables 6 and 7). The first to the fifth infralabials are relatively stable and most variation takes place behind this area. The variation in number of infralabials posterior to the fifth is more erratic and involves the addition, deletion, fusion, and division of small scales. Thus, the pattern is not clear. Division and fusion, however, do take place within this relatively stable anterior zone. Increase in the number of infralabials in this area most commonly involves the division of the third infralabial (82.4%), but also may involve the division of the fourth (11.8%) or second (5.8%) infralabials. Decrease in the number of infralabials in this area most often involves the fusion of the third and fourth infralabials (71.4%), but also may involve the fusion of the second and third infralabials (28.6%). Variation in these scales is shown in Tables 6 and 7.

Nasal.—The nasal scale is always divided vertically. A few specimens, however, have the postnasal section divided horizontally.

Loreal.—The loreal usually is single on both sides of the head (97.4%). Increase in the number of loreals involves the hori-

zontal division of the existing loreal into two parts on one or both sides of the head and the addition of one or more smaller scales, usually between the loreal and the supralabials. Decrease in the number of loreals involves the fusion of this scale either with the prefrontal (50.0%) or with the posterior nasal (50.0%). Variation in this scale is shown in Table 8.

Preoculars.—The number of preoculars usually is 2 (98.9%). Increase in the number of preoculars involves either the formation of a suture at the junction of the canthal ridge on this scale and the flat vertical portion (28.6%), the formation of a suture farther down on the vertical portion of this scale (28.6%), or the splitting off of a scale from the fourth supralabial to form a third preocular-like scale (42.8%). Decrease in the number of preoculars is an uncommon event, but when it occurs it involves the fusion of the lower preocular with the third infralabial. Variation in these scales is shown in Table 9.

Postoculars.—The numbers of postoculars predominantly is 2 (98.0%). Increase in the number of postoculars involves the formation of a suture either in the middle of the lower postocular or in the middle of the upper postocular, or involves the fusion

TABLE 9.
Variation in numbers of preoculars in *Masticophis flagellum*.

Subspecies	1-1	1-2	2-2	2-3	3-3	3-4	Total
<i>flagellum</i>	—	—	342	1	—	—	343
<i>testaceus</i>	—	—	528	4	1	—	533
<i>lineatulus</i>	—	—	33	—	—	—	33
<i>piceus</i>	—	—	246	3	2	—	251
<i>cingulum</i>	1	—	77	1	—	—	79
<i>ruddocki</i>	—	—	11	—	—	1	12
<i>fuliginosus</i>	—	1	70	—	—	—	71
TOTAL	1	1	1307	9	3	1	1322

TABLE 10.
Variation in number of postoculars in *Masticophis flagellum*.

Subspecies	1-1	1-2	2-2	2-3	3-3	Total
<i>flagellum</i>	1	1	337	2	1	342
<i>testaceus</i>	5	5	516	3	1	530
<i>lineatulus</i>	—	—	33	—	—	33
<i>piceus</i>	—	—	255	1	—	256
<i>cingulum</i>	—	—	79	—	—	79
<i>ruddocki</i>	—	—	12	—	—	12
<i>fuliginosus</i>	1	—	69	2	4	76
TOTAL	7	6	1301	8	6	1328

of the two normal postoculars and the splitting off of two scales from the fifth supralabial. Decrease in the number of postoculars involves either the fusion of the upper postocular with the parietal, the fusion of the two postoculars into one scale, or the fusion of the lower postocular with the fifth supralabial. Variation in these scales is shown in Table 10.

Frontal.—The frontal normally is bell shaped. The only anomaly observed in this scale is the presence, in two specimens, of a suture through the middle of the scale dividing it into anterior and posterior portions.

Internasals.—These scales normally are paired. One specimen (NCSM 5886), however, has the right internasal split into right and left halves and the left internasal fused with the anterior nasal.

Prefrontals.—These scales are normally paired. One specimen, however, has the prefrontal area divided into three scales.

Body Scutellation

Ventrals.—The number of ventrals ranges from 173 (in *M. f. testaceus*) to 212 (in *M. f. flagellum*). Ranges for the various subspecies are listed in the appropriate subspecies account. The means of the populations east of the Mississippi River are relatively constant. All means fall within the range of 201.0 to 203.7 for males and 196.0 to 201.8 for females. The highest means are in Florida, southern Georgia, Alabama, Mississippi, and western South Carolina (Fig. 26). West of the Mississippi River the mean number of ventrals drops sharply and continues to decrease more gradually through central and southern Texas (Fig. 27). In western Texas the means again be-

gin to rise, abruptly so in eastern New Mexico. The mean continues to rise through western New Mexico but again begins to decrease in Arizona, Nevada, Utah, and portions of southern California. Both to the north and the south of Los Angeles, San Bernardino, and Riverside counties, California, the mean number of ventrals again increases. Immediately to the south of San Diego and Imperial counties, California, the ventral number decreases, but farther down the peninsula of Baja California the mean number increases, until in the cape region the mean number of ventrals approaches some means for southeastern United States, the area which has the highest mean number of ventrals (Fig. 28). In Sonora the mean number of ventrals increases from north to south, but this cline reverses itself in northern Sinaloa. To the east of the Sierra Madre Occidental, in Chihuahua, the mean number of ventrals is much lower than to the west and most closely resembles means for central Texas. To the south, in Durango and Zacatecas, the mean is similar to that in Chihuahua but is slightly less than the mean of populations to the east in San Luis Potosí and Tamaulipas. There is a minor amount of sexual dimorphism in ventral number but females often have slightly fewer than males.

Anal Plate.—The anal plate is normally divided in this species and only two of the specimens examined have the two halves fused.

Subcaudals.—The variational trends in subcaudals are less clear than for the ventrals primarily because only about 48% of the specimens examined have complete tails. The number of subcaudals ranges from 91 (in *M. f. flagellum*) to 129 (in *M. f. fuliginosus*).

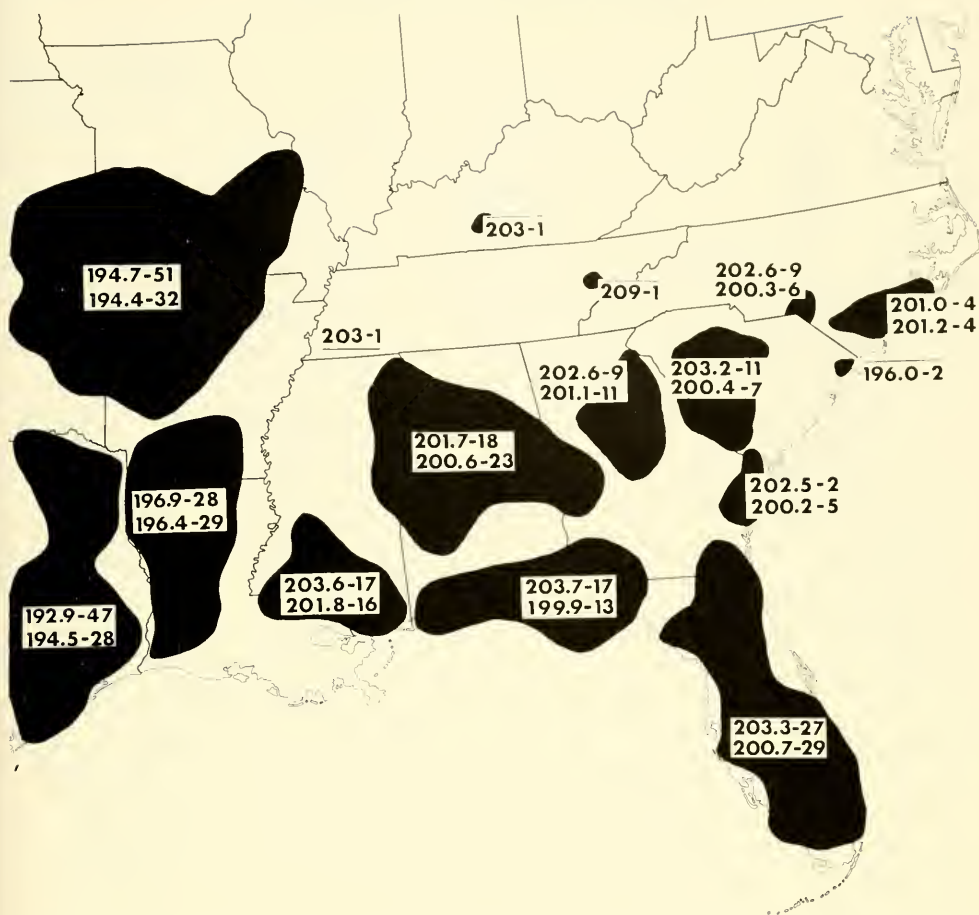


Figure 26. Geographic variation of ventral number in *Masticophis flagellum* in the eastern United States. Black blotches represent the areas from which samples were taken. The upper numbers associated with each blotch are the sample mean and sample size (separated by a dash) for males; the lower numbers present the same data for females. When a line appears in place of either the upper or lower figures, it signifies that no specimens of that sex were present in the sample.

Variational trends are similar to those observed for ventrals but are not identical. The mean number of subcaudals east of the Mississippi River is relatively high, but means for various populations are not so constant as are those of the ventrals in this area (Fig. 29). West of the Mississippi River the mean number of subcaudals decreases rather sharply and continues to decrease through western Oklahoma and eastern and central Texas (Fig. 30). Except for an increase in the male mean in eastern New Mexico, the decrease continues in western New Mexico and Arizona. The mean in-

creases again in southern California, except for populations from the central valley and adjacent areas where there are fewer subcaudals. The mean continues to increase, with some variation, southward through the peninsula of Baja California; means for the southern portion of the peninsula are the highest anywhere within the range (Fig. 31). In Sonora the mean tends to decrease from north to south, rather than increase as does the mean for the ventrals. This trend continues into northern Sinaloa where the mean is the lowest anywhere within the range, with the exception of Chihuahua



Figure 27. Geographic variation of ventral number in *Masticophis flagellum* in the western United States. Explanation as for Figure 26.

where the female mean is lower than that for females from northern Sinaloa. Although based on relatively few counts, the mean number of subcaudals for central and eastern Mexico is similar to that for central and southern Texas.

Sexual dimorphism in subcaudals is evident, with males having, usually, a higher mean number. The amount of difference between the sexes varies from population to population and ranges from about 2 to 8 scales in the majority of populations.

Apical Pits.—The number of apical pits in *Masticophis flagellum* is 2 over most of the body. I examined the shed skin of a *M. f. piceus* and found that not all dorsal body scales have 2 apical pits nor do all have apical pits. In the neck region

scale pits are present on all rows except the first two lateral rows. On most scales the number of pits is 2, but on some scales there is only 1. On the other scales the two apical pits show varying degrees of divergence. On a few scales scattered along the dorsum there are no pits. On the anterior portion of the body there are no pits on the first two lateral rows and on the third they appear but faintly. The pits are more prominent dorsad. At midbody there are no pits on rows 1 through 4 and they appear but faintly on row 5. In the anal region few scales have apical pits. No pits are present on the scales of the tail.

Dorsal Scale Rows.—The dorsal scale rows in *Masticophis flagellum* are normally 19-17-15-14-13. This pattern includes two lat-

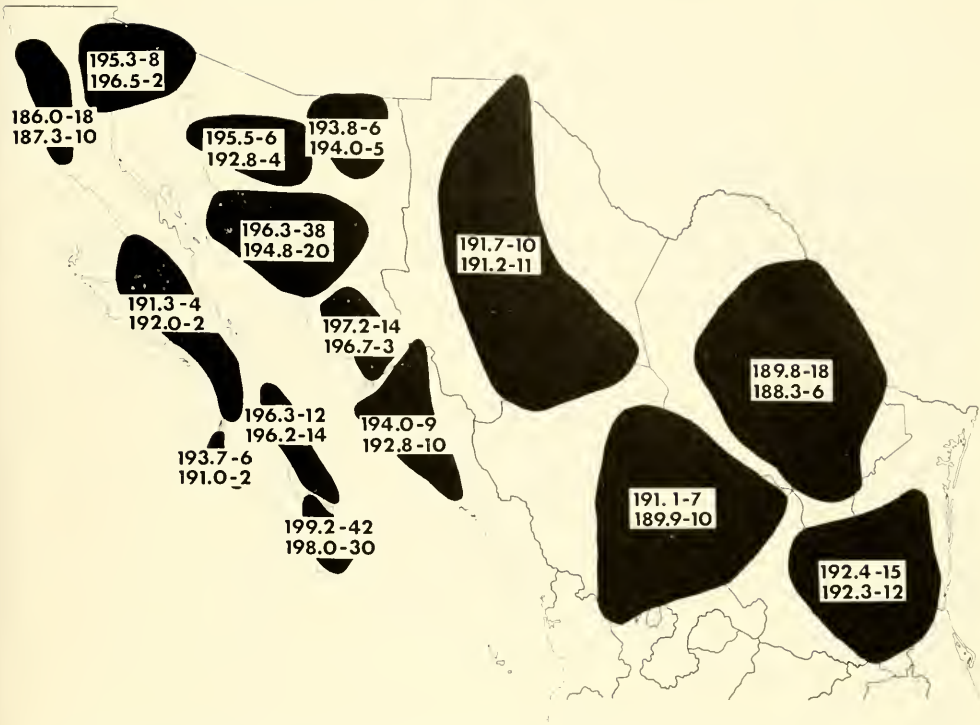


Figure 28. Geographic variation of ventral number in Mexico. Explanation as for Figure 26

eral reductions and two middorsal reductions. Scale reduction patterns were determined for 461 specimens from all portions of the range, including 339 from the United States and 122 from Mexico. Approximately 20% of the patterns may be summarized as follows:

$$\begin{array}{l} 19 \frac{3+4 (6-35)}{3+4 (6-33)} \quad 17 \frac{3+4 (85-139)}{3+4 (86-142)} \\ 15 \frac{7+8 (91-159)}{7+8 (98-174)} \quad 14 \frac{7+8 (98-174)}{7+8 (98-174)} \quad 13 \end{array}$$

Several distinctive types of deviations from the standard pattern given above were noted. These deviations may be grouped as follows:

1. Lateral Reduction Substitution. In this pattern fusion of rows 2 and 3 or 4 and 5 replaces that normally occurring between rows 3 and 4. This substitution may occur in either the first or second lateral reduction as shown in the following examples:
AU 409 (Alabama)

$$\begin{array}{l} 19 \frac{4+5 (14)}{4+5 (16)} \quad 17 \frac{3+4 (138)}{3+4 (138)} \\ 15 \frac{7+8 (168)}{7+8 (156)} \quad 14 \frac{7+8 (168)}{7+8 (156)} \quad 13 \end{array}$$

UAZ 9336 (Sonora)

$$\begin{array}{l} 19 \frac{3+4 (13)}{3+4 (13)} \quad 17 \frac{4+5 (113)}{4+5 (112)} \\ 15 \frac{8+9 (116)}{8+9 (116)} \quad 14 \frac{7+8 (122)}{7+8 (122)} \quad 13 \end{array}$$

Fifty specimens (10.9%) show this deviation in the first lateral reduction and 51 (11.1%) show it in the second lateral reduction.

2. Occurrence of First and/or Second Middorsal Reductions Anterior to Second Lateral Reduction. This type of pattern is relatively common (41.2%), although it is more common for the first middorsal reduction to appear anterior to the second lateral reduction (34.2%). The two types of patterns are illustrated by the following examples:
MCZ 12779 (Alabama)

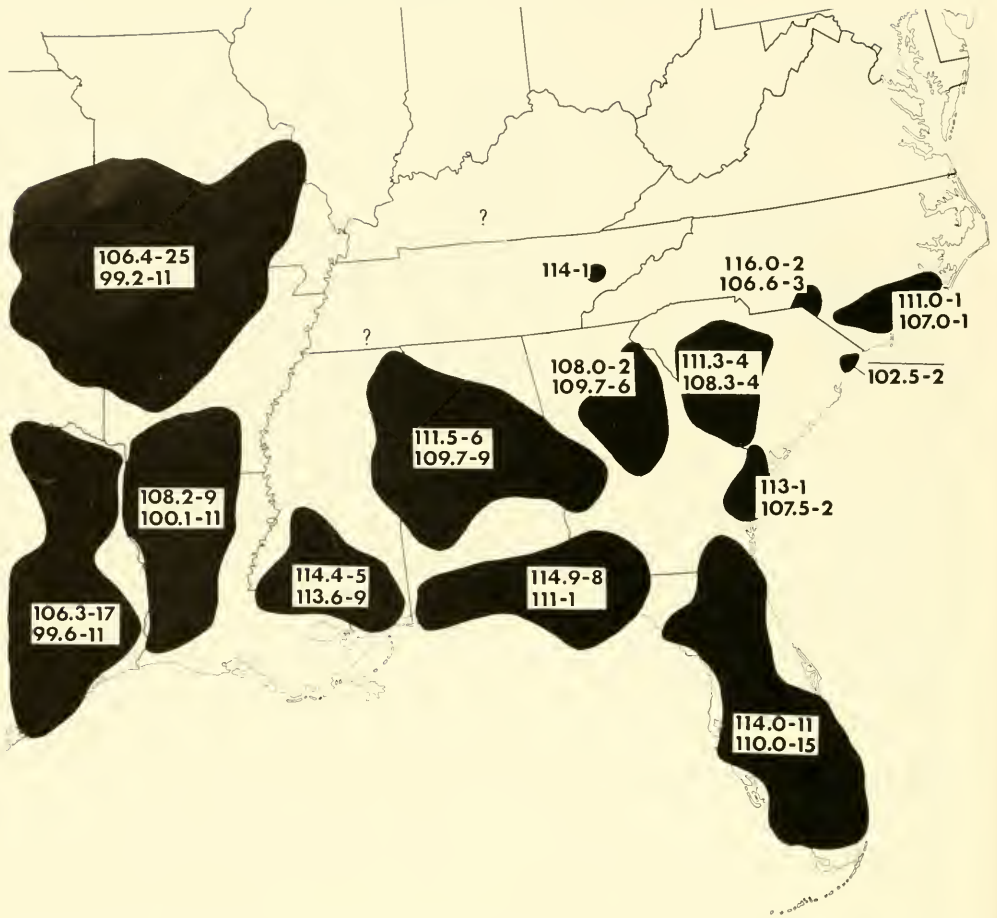


Figure 29. Geographic variation of subcaudal number in the eastern United States. Explanation as for Figure 26.

$$19 \frac{3+4 (12)}{3+4 (14)} \quad 17 \frac{8+9 (128)}{8+9 (128)}$$

$$16 \frac{3+4 (128)}{3+4 (130)} \quad 14 \frac{7+8 (156)}{7+8 (156)} \quad 13$$

NCSM 5872 (Mississippi)

$$19 \frac{3+4 (14)}{3+4 (15)} \quad 17 \frac{8+9 (132)}{8+9 (132)}$$

$$16 \frac{8+9 (139)}{8+9 (139)} \quad 15 \frac{3+4 (140)}{3+4 (145)} \quad 13$$

An example of this type of pattern is presented below:

NCSM 5170 (North Carolina)

$$19 \frac{3+4 (8)}{3+4 (9)} \quad 17 \frac{3+4 (127)}{3+4 (125)}$$

$$15 \frac{6+7 (142)}{6+7 (142)} \quad 14 \frac{6+7 (145)}{6+7 (145)}$$

$$13 \frac{6+7 (175)}{6+7 (175)} \quad 12$$

3. Lateral Displacement of the First and/or Second Middorsal Reductions. This pattern is characterized by the substitution of the fusion of scale rows 6 and 7 on either side of the body for the usual 7 + 8 fusion. This substitution is relatively common, occurring in 34.1% of the patterns determined.

4. Preanal Decrease. In this pattern there is a further decrease from the usual number of thirteen scale rows at the anus to twelve. This occurs in 38.9% of the patterns determined and involves usually a middorsal fusion of rows 6 and 7. An example is shown below:

UCM 19721 (Colorado)



Figure 30. Geographic variation of subcaudal number in the western United States. Explanation as for Figure 26.

$$\begin{array}{r} 19 \frac{3+4(12)}{3+4(17)} \quad 17 \frac{3+4(114)}{3+4(115)} \\ 15 \frac{7+8(116)}{7+8(124)} \quad 14 \frac{7+8(124)}{7+8(124)} \\ 13 \frac{6+7(148)}{6+7(148)} \quad 12 \end{array}$$

5. Preanal Increase. This type of pattern is characterized by an increase from thirteen rows to fourteen or fifteen rows or from fourteen rows to fifteen or sixteen rows. This increase may take place either by a lateral or middorsal division of one scale row into two. This deviation occurs in 4.6% of the patterns. An example is shown below:
UNM 8329 (Texas)

$$19 \frac{3+4(17)}{3+4(14)} \quad 17 \frac{3+4(118)}{3+4(118)}$$

$$\begin{array}{r} 15 \frac{7+8(129)}{7+8(129)} \quad 14 \\ 7+8(132) \quad 13 \frac{3=3+4(188)}{2=2+3(187)} \quad 15 \end{array}$$

6. Sporadic Increase and Decrease. In this pattern there is an irregular increase and decrease of dorsal scale row number at various points along the body. This deviation occurs in 2.0% of the patterns. An example is shown below:
CM 9533 (South Carolina)

$$\begin{array}{r} 19 \frac{3+4(9)}{?} \quad 17 \frac{3+4(127)}{3+4(128)} \quad 15 \frac{7+8(135)}{7+8(135)} \\ 14 \frac{7+8(145)}{7+8(145)} \quad 13 \frac{6+7(169)}{6+7(169)} \\ 12 \frac{2+3(177)}{2+3(177)} \quad 11 \frac{2=2+3(178)}{2=2+3(178)} \\ 12 \frac{2+3(181)}{2+3(181)} \quad 11 \frac{2+3(186)}{2+3(186)} \end{array}$$



Figure 31. Geographic variation of subcaudal number in Mexico. Explanation as for Figure 26.

$$10 \frac{2 = 2 + 3 (191)}{2 = 2 + 3 (199)} \quad 11 \frac{2 + 3 (192)}{2 = 2 + 3 (201)}$$

7. Simultaneous Paravertebral Fusion. Fusion of rows 6 and 7 on both sides of the body at the same place replaces the first two middorsal reductions. This deviation occurs in 3.7% of the patterns. An example of this type of pattern is shown below:

UMMZ 79621 (Arkansas)

$$19 \frac{?}{3 + 4 (13)} \quad 17 \frac{3 + 4 (119)}{3 + 4 (117)}$$

$$15 \frac{6 + 7 (130)}{6 + 7 (131)} \quad 13$$

8. Fusion of Middorsal with Two Paravertebral Scales. Fusion of rows 6, 7, and 8 at one spot replaces the normal first two middorsal reductions in 0.9% of the patterns as shown below:

MCZ 12778 (Alabama)

$$19 \frac{3 + 4 (9)}{3 + 4 (9)} \quad 17 \frac{3 + 4 (116)}{3 + 4 (116)}$$

$$15 \frac{6 + 7 + 8 (128)}{6 + 7 + 8 (128)} \quad 13$$

The variation exhibited by the individual

components of the scale reduction pattern will be considered next.

First Lateral Reduction. The reduction from 19 to 17 rows most commonly involves the fusion of the third and fourth scale rows (93.1% of the patterns determined exhibit this condition), but may also involve the fourth and fifth rows (4.8%) or the second and third rows (2.1%). The range in point of reduction is from the 4th to the 35th ventral (mean 11.6).

Second Lateral Reduction. The reduction from 17 to 15 rows most commonly involves the fusion of the third and fourth scale rows (92.9%), but may also involve the fusion of the fourth and fifth (6.3%) or the second and third rows (0.8%). The range in point of reduction is from the 85th to the 173rd ventral (mean 118.5).

First Middorsal Reduction. The reduction from 15 to 14 rows most commonly involves the fusion of the seventh and eighth rows (50.0%), but may also involve the fusion of the eighth and ninth rows (when the first middorsal reduction occurs anterior to the second lateral reduction) (27.1%),

the seventh and eighth rows counting from the right side (7.7%), the sixth and seventh rows (4.2%), or a miscellaneous number of rows (11.0%). Occurrence of the first middorsal reduction anterior to the second lateral reduction takes place in 34.2% of the patterns determined. In 7.0% of the patterns the second middorsal reduction also occurs anterior to the second lateral reduction.

Second Middorsal Reduction. The reduction from 14 to 13 scale rows most frequently involves the fusion of the seventh and eighth rows (67.8%), but may also involve the eighth and ninth rows (when the second middorsal reduction occurs anterior to the second lateral reduction) (5.1%), the sixth and seventh rows on the right (2.9%) or the left (16.9%), or a miscellaneous number of rows (7.3%). The range in point of reduction is from the 98th to the 191st ventral (mean 129.5).

Third Middorsal Reduction. The reduction from 13 to 12 rows most commonly involves the fusion of the sixth and seventh rows (98.2%), but may also involve the sixth and seventh rows on the right side (1.8%). The range in point of reduction is from the 130th to the 194th ventral (mean 160.7).

Geographical Aspects of the Dorsal Scale Reduction Formula

Most of the types of deviation from the standard pattern have no geographic significance or have a very low frequency of occurrence within the species. These deviations include the lateral reduction substitution, occurrence of the second middorsal reduction anterior to the second lateral reduction, lateral displacement of the first and second middorsal reduction, preanal increase, sporadic increase and decrease, simultaneous paravertebral fusion, and fusion of the middorsal with two paravertebral scales. The geographic variation exhibited by the percentage of occurrence of the first middorsal reduction anterior to the second lateral reduction is highly erratic (Table 11). Adjacent states often have very different percentage values. For example, Mississippi has a value of 66.7%, but Louisiana has a value of only 10.0%. Likewise, Arkansas has a value of 16.7%, but Missouri has a value of 52.6%. Although this character is geo-

graphically variable there apparently is no consistent pattern.

Another geographically variable aspect of the scale reduction pattern is the frequency of reduction to twelve scales anterior to the vent (Table 11). Much of this variation is also erratic, except that the subspecies *lineatulus* characteristically has a high frequency of preanal decrease to 12 rows. Of the patterns determined for this subspecies, 90.6% had this deviation. In contrast, the values for Texas and Tamaulipas are 22.7% and 20.0%, respectively. Interestingly enough, those areas immediately adjacent to the range of *M. f. lineatulus* also have high values. The value for Coahuila is 68.4%, from which state I determined patterns of 17 *testaceus* and two *lineatulus*. In New Mexico, where *lineatulus* and *testaceus* intergrade over a large area, 11 out of the 12 *lineatulus* × *testaceus* intergrades examined have 12 rows at the vent, while only two out of eight *testaceus* have this condition.

Proportions

Relative Tail Length.—The relative tail length changes little during ontogeny and there is likewise little difference between the sexes. The mean for the tail length/total length ratios for snakes under 900 mm in total length is 0.249, for those over 900 mm it is 0.248. The means for this ratio for males and females of the seven subspecies are as follows (males listed first, females second; the number in parentheses following the mean value for the tail length/total length ratios is the number of observations): *flagellum*—0.248 (65), 0.247 (82); *testaceus*—0.246 (36), 0.244 (45); *lineatulus*—0.241 (29), 0.243 (17); *piceus*—0.252 (83), 0.258 (77); *cingulum*—0.247 (33), 0.253 (20); *ruddocki*—0.253 (3), 0.257 (1); *fuliginosus*—0.256 (37), 0.261 (27). A slight amount of geographic variation is indicated in the above data. Snakes from the western portion of the range of the species have longer tails than those snakes from the eastern portions of the range.

Hemipenis

The following description was taken from the two organs of UG 431. Each hemipenis is bilobed with a single, oblique sulcus sper-

TABLE 11
Percent frequency of deviations observed in the scale reduction pattern of *Masticophis flagellum*.

State	1°		2		3		4		5		6		7		8	
	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B
Florida	14.3	9.5	33.3	—	—	—	4.8	—	19.0	—	—	—	—	—	—	—
Georgia	5.0	10.0	25.0	10.0	—	—	15.0	25.0	42.9	19.0	—	—	—	—	—	—
Alabama	38.5	23.1	23.1	—	—	—	30.8	23.1	45.0	15.0	—	—	—	—	—	—
Mississippi	16.7	16.7	66.7	16.7	—	—	25.0	16.7	38.5	7.7	—	—	—	—	—	7.7
South Carolina	28.6	14.3	—	—	—	—	28.6	28.6	33.3	8.3	—	—	—	—	—	—
North Carolina	6.3	6.3	18.8	—	—	—	18.8	25.0	71.4	14.3	14.3	—	14.3	—	—	—
Kentucky	100.0	—	—	—	—	—	100.0	—	37.5	—	—	—	6.3	—	—	—
Tennessee	100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Louisiana	5.0	15.8	10.0	—	—	—	20.0	35.0	20.0	—	—	—	10.0	—	—	—
Missouri	—	—	52.6	15.8	—	—	10.5	21.1	42.1	5.3	—	—	—	—	—	—
Illinois	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Arkansas	—	5.6	16.7	5.6	—	—	—	22.2	27.8	11.1	—	—	11.1	—	—	—
Kansas	13.3	20.0	13.3	—	—	—	13.3	13.3	13.3	—	—	—	—	—	—	—
Nebraska	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Oklahoma	10.0	25.0	30.0	—	—	—	5.0	35.0	35.0	5.0	5.0	—	10.0	—	—	—
Texas	4.5	—	22.7	4.5	—	—	9.1	13.6	22.7	18.2	—	—	—	—	—	—
Colorado	—	20.0	30.0	5.0	—	—	20.0	15.0	40.0	5.0	—	—	10.0	—	—	—
Tamaulipas	20.0	10.0	—	—	—	—	—	30.0	20.0	—	—	—	—	—	—	—
Veracruz	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Nuevo Leon	—	25.0	—	—	—	—	—	—	50.0	25.0	—	—	—	—	—	—
San Luis Potosí	11.1	—	22.2	11.1	—	—	33.3	11.1	55.5	—	44.4	—	11.1	—	—	—
Coahuila	15.8	21.1	42.1	—	—	—	5.3	15.8	68.4	—	5.3	—	—	—	—	—
Chihuahua	7.1	—	50.0	—	—	—	21.4	21.4	92.9	—	—	—	—	—	14.3	—
Durango	10.0	20.0	60.0	20.0	10.0	—	10.0	10.0	90.0	—	—	—	—	—	—	—
Zacatecas	50.0	—	50.0	—	—	—	—	—	50.0	—	—	—	—	—	—	—
New Mexico	20.0	10.0	40.0	5.0	10.0	—	—	15.0	65.0	—	—	—	20.0	—	—	—
Utah	—	7.7	46.2	7.7	7.7	—	7.7	15.4	7.7	—	—	—	—	—	—	—
Nevada	9.1	13.6	36.4	13.6	9.1	—	9.1	18.2	36.4	—	—	—	4.5	—	—	4.5
California	14.8	7.4	59.3	18.5	14.8	—	11.1	18.5	11.1	3.7	—	—	—	—	—	—
Arizona	10.3	13.8	44.8	10.3	37.9	—	20.7	20.7	24.1	—	—	—	—	—	—	—
Sonora	9.1	9.1	54.5	13.6	9.1	—	18.2	18.2	36.4	—	4.5	—	—	—	—	—
Sinaloa	15.4	7.7	23.1	—	—	—	7.7	7.7	7.7	—	—	—	—	—	—	—
Baja California	11.1	5.6	33.3	5.6	22.2	—	27.8	27.8	33.3	—	—	—	11.1	—	—	—

* The numbers 1 through 8 refer to types of deviations seen in the scale reduction formula. The letters refer to subdivisions within the major types of deviations. 1—Lateral reduction substitution; A—substitution appears in first lateral reduction, B—substitution appears in second lateral reduction. 2—Occurrence of first and/or second middorsal reductions anterior to second lateral reduction; A—first middorsal reduction, B—second middorsal reduction. 3—Lateral displacement of first and/or second middorsal reductions; A—first middorsal reduction, B—second middorsal reduction. 4—Preanal decrease. 5—Preanal increase. 6—Sporadic increase and decrease. 7—Simultaneous paravertebral fusion. 8—Fusion of middorsal with two paravertebral scales. The numbers in the body of the table are percentages.

maticus extending onto the left lobe of the organ. Distally each organ is covered with calyces in about 13 rows on the sulcate side and about 9 rows on the absulcate side. The micro-ornamentation of the calyces is spinulate. The apex of the organ is smooth. The proximal area is spinose, the spines increasing in size proximally. There are about 6 rows on the absulcate side, 4 on the sulcate side. Two enlarged basal spines are present, one on either side of the sulcus spermaticus. The lateral spine is the larger. The basal area is naked save for some very small, scattered spinules.

The *in situ* hemipenis extends about to the level of subcaudal 11 (range 6-13).

Anal Sacs

The anal sacs extend about to the level of subcaudal 5 (range 4-6). The length of anal sacs was determined for only 21 specimens and the degree of sexual dimorphism, if any, is slight (average of 5.17 for males, 5.36 for females).

Dentition

Very few tooth counts were made and the majority of those were made on the maxilla. The number of teeth on the maxilla ranges from 16 to 21 (mean 18.6). Observed ranges and means for the number of teeth on the other dentigerous bones are as follows: palatine—12 to 15 (13.3); pterygoid—17 to 25 (21.0); dentary—19 to 24 (21.7).

Umbilicus

The number of scales involved in the umbilical scar ranges from 2 to 7 (mean 3.7). The beginning point of the umbilical scar ranges from the 146th to the 185th ventral (mean 164.4). The position of the umbilical scar is not sexually dimorphic as suggested by Edgren (1951) for *Heterodon platyrhinos*, but rather is related to the total number of ventrals. Thus, if there was much sexual dimorphism in the number of ventrals in *Masticophis flagellum*, which there is not, the position of the umbilical scar would reflect that dimorphism if considered alone and without relation to the total number of ventrals (see Martof, 1954, for a discussion of the position of the umbilical scar in *Thamnophis s. sirtalis*).

DISTRIBUTION AND HABITAT

Masticophis flagellum inhabits relatively dry, warm situations ranging from the deserts of the southwestern United States to the pine forest of the southeastern United States. This snake occurs in the southern half of the United States from coast to coast, thence south into Mexico the length of the peninsula of Baja California and as far south as Sinaloa on the west coast, Zacatecas on the central plateau, and extreme northern Veracruz on the east coast (Figs. 2 and 3).

In Florida *M. f. flagellum* is distributed throughout the state. Carr (1940) reported the coachwhip as an occasional inhabitant of wire-grass flatwoods, palmetto flatwoods, upland hammock, and a frequent inhabitant of limestone flatwoods, rosemary scrub, and highpine. Carr also noted that "although alert and very active creatures, coach-whips are frequently killed by groundfires in the flatwoods, more often apparently than any other snake; I once found seven dead after a fire which burned ten or twelve acres of flatwoods in Collier County." Charles W. Myers (*in litt.*) gave the following information regarding habitat distribution in Florida: "It was my impression that they are most common in Coastal Scrub vegetation . . . , but they also occur in Pine Flatwoods, Mixed Pine-hardwood Forest, and Mesophytic Hammock. One of the scrub specimens was almost in the Grassy Beach Front and I have no doubt that they also prowl that environment." In southern Florida, Duellman and Schwartz (1958) found that "most of the specimens of *Masticophis* come from the eastern rim [as opposed to the interior lowlands] where they are found in the pine woods. One has been found on a sandy island off the Gulf coast and another at Pinecrest, an isolated pine 'island' in the Everglades. These snakes have never been observed in the Everglades."

There is only scanty information available on the habitat distribution of *M. f. flagellum* in the states of Georgia, North and South Carolina, and Alabama. Martof (1956) reported the distribution in Georgia as statewide and the habitat as "rock piles in fields, open woods." Charles W. Myers (*in litt.*) stated that he has collected specimens in "rolling farm and pasture land" and an "overgrown field on river floodplain" in

Georgia. Löding (1922) remarked that in Alabama the eastern coachwhip is "not uncommon in dry fields and cut-over pine lands in Mobile County" and that he has seen "this snake in pine forest on and near the mountains in Cleburne and Clay counties." Myers (*in litt.*) reported that he collected an Alabama specimen that was "... dug from a small mammal burrow in grassy pinewoods." Collector's field notes accompanying specimens in the North Carolina State Museum from North Carolina indicate the following habitat designations: "sandy, open field" and "plum thicket." DePoe, Funderburg, and Quay (1961) gave the distribution of the eastern coachwhip in North Carolina as the southern half of the Coastal Plain. This information is borne out by the specimens I have examined.

The single specimen available from Kentucky was collected in a "broomsage field" (Chenoweth, 1949).

I have seen only two specimens from Tennessee, one from Knoxville, Knox County (the locality data may be in error as the area is relatively mountainous), and one from 3 miles E Hornsby, Hardeman County. In reference to the distribution of the coachwhip within the state, Glenn Gentry (*in litt.*) wrote that "in my 30 years of miscellaneous collecting I have talked with many natives throughout the state and most of them (especially the older people) has heard the 'folk tales' about the coachwhip snake and/or had seen them. The same was true of the ground rattler and the bull (pine) snake. The distribution of the last two in particular is very spotty. Evidently the destruction of timber and cultivation have severely reduced the suitable habitat for these and no doubt to some extent for the coachwhip."

Cook (1954) stated that the distribution in Mississippi is state wide, "including all faunal regions."

Fitch (1949) noted that in western Louisiana *M. flagellum* occurs "in all habitats, especially dry uplands, often near cultivated areas." Strecker and Frierson (1926) dug one out of a hole in the bank of Wallace Bayou, a bayou separating a portion of DeSoto and Caddo parishes. My own experience with the coach whip in Louisiana is rather limited, primarily because the species is relatively uncommon in the state. I have

found the species in the longleaf pine hills of central and west-central Louisiana. Locality data for specimens I have examined from the state indicate that it is found, in addition to the habitat mentioned above, in the longleaf pine hills of the upper tier of Florida parishes, the shortleaf pine-oak-hickory hills of northwestern and north-central Louisiana, and a few have been collected in the prairie region in southwestern Louisiana. The species is missing from the marshland of southern Louisiana.

Very little information is available on the habitat distribution of *M. f. flagellum* in Arkansas. Dowling (1956) stated that the coachwhip snake is found in the Ozark Plateau, Arkansas River valley, and Ouachita Mountain region, and later (1957) expanded the range to include the entire state. Available locality records suggest that this snake is found everywhere in Arkansas except for the Mississippi alluvial plain of eastern Arkansas. A specimen (LSUMZ 14145) collected 2 miles SE Gamaliel, Baxter County, was noted by the collector to have come from "hardwood forest in mountains."

Anderson (1965) stated that "coachwhips occur in Missouri in rough, rocky terrain in rather exposed situations. They have also been observed in open grassy areas on timbered hillsides and in low bushes." Locality records indicate that *flagellum* occurs in the southwestern Missouri prairie and the Ozark region (Anderson, 1965, p. xiv).

The few specimens collected in Illinois have come from the lower Mississippi border counties in the Mississippi River bluff and dissected upland (Smith, 1961).

Smith (1950) stated that "this terrestrial species is usually found in grassy areas more or less devoid of trees . . ." in Kansas. Taylor (1929) and Brennan (1934) noted that the western coachwhip is usually found in open prairie country in Kansas.

Force (1930) reported that in the region of Tulsa County, Oklahoma, the eastern coachwhip is "common on sunny slopes, under rocks and in brush piles." The eastern coachwhip is found mainly in the oak-hickory hardwood forest of eastern Oklahoma and the western coachwhip in the tall-grass and short-grass areas of western Colorado.

The coachwhip occupies all types of habitat in Texas. I have already mentioned the vegetation types which *M. f. flagellum* inhabits in eastern Texas. Brown (1950) indicated that the western coachwhip is found in the following "natural regions": Trans-Pecos—a high plateau, the vegetation of which is typically Chihuahuan Desert in type, *i.e.*, desert scrub with creosote bush, yucca, lechuguilla, sotol, and several species of cacti. High Plains—a level to slightly rolling plain in the Panhandle, the primary vegetation of which is short and bunch grasses with scattered shrubs and mesquite in some areas. North Central Plains Region—a rolling plain in the north central portion of the state, the predominant vegetation of which is bunch and short grasses with scattered timber, mostly post oak, blackjack oak, and mesquite. Edwards Plateau—a limestone plateau with a rolling topography and a vegetation cover composed primarily of short grasses with scattered live oaks, shin oak, and cedar. Rio Grande Embayment—a rolling plain with some open prairie with a chaparral type of vegetation, with the exception of the grassy prairies, composed of mesquite, acacia, mimosa, prickly pear, and other cacti. *M. f. testaceus* also occurs marginally in the Coastal Prairie, a grass-covered plain with coarse grasses predominating, the Post Oak Belt, a region of rolling hills and a few prairies with post oak and other hardwoods dominant on the uplands and bunch and short grasses in the prairies. It is this latter area where *M. f. flagellum* and *M. f. testaceus* intergrade (information on Texas vegetation compiled from Brown, 1950; McDougall and Sperry, 1951; and Raun, 1965).

In addition, Fouquette and Lindsay (1955) noted that *M. f. testaceus* occurred in Dawson and Hutchinson counties in the Panhandle most commonly in the flood plain association, and that it also was found in deep sand and on rocky slopes. In Terrell County, Milstead, Mecham, and McClintock (1950) reported that "three specimens were collected in the cedar savannah, 15 in the mesquite-creosote, three in the mesquite-sumac-condalia, and two in the live-oak association." Jameson and Flury (1949) stated that in the Sierra Vieja Range of Presidio County the western coachwhip is more common "in the Plains belt than in the Roughland belt. Of 10 specimens collected, only

two were from the Roughland belt. One of these was in the stream bed association, and the other was in the lechuguilla-beargrass association on top of the mesa. Specimens from the Plains belt were from the following associations: catclaw-tobosa, four; creosote-bush-catclaw-blackbush, one; mesquite-huisache-blackbush, one; and yucca-tobosa, one." In the Black Gap Wildlife Management Area in eastern Brewster County, Axteell (1959) found seven specimens, five of which came from the floodplain, one from the stream bed, and one from the low, limestone gravel hills.

In Colorado the distribution of *M. f. testaceus* is limited to the short-grass areas east of the Rocky Mountains.

In New Mexico *M. f. testaceus* is found mainly in the short-grass areas of eastern New Mexico. This subspecies intergrades with *lineatulus* over the broad expanse of mesquite grassland and Chihuahuan Desert in central and southwestern New Mexico. Gehlbach (1965) mentioned a *M. f. lineatulus* × *testaceus* intergrade which came "from the Plains Life Belt at 6300 feet, where narrow-leaved yucca and one-seed junipers are prevalent." In the Tularosa Basin of western Otero and eastern Dona Ana counties, Lewis (1950) found *M. f. testaceus* (most likely *lineatulus* × *testaceus* intergrades) in the yucca grassland zone and the *Atriplex* (saltbush)-*Allenrolfea occidentalis* (iodine bush) association.

The habitat distribution of *Masticophis flagellum* in Mexico has been little studied. With respect to *M. f. testaceus*, Martin (1958) stated that in southern Tamaulipas this snake is found in the thorn forest, and areas "characterized by low trees and shrubs, usually thorny and deciduous, and either microphyllous or compound-leaved," and the low tropical deciduous forest "formed of trees of medium height (12-15 m.) which are rather widely spaced and rise out of a dense, almost impenetrable, understory of lower trees, about 5 m. in height."

A large portion of the range of *M. f. lineatulus* lies within the boundaries of the Chihuahuan Desert in the Mesa del Norte section of the Central Mexican Plateau. This desert is characterized by the presence of low shrubs and lies mostly above 3500 ft in elevation (Lowe, 1964). The main shrubs are *Larrea tridentata* (creosotebush), *Acacia*

cymbispina, *Flourensia cernua* (tarbush), and *Prosopis juliflora* (mesquite in shrub form). Low leaf succulents such as *Agave lechuguilla* (lechuguilla), *Agave falcata*, and *Hechtia* sp. (a member of the family Bromeliaceae) are also present. Several species of *Yucca* are also represented (Shreve and Wiggins, 1964).

Some information on habitat distribution of the subspecies of *Masticophis flagellum* in Arizona has already been discussed in the section on *M. f. lineatulus*. The main portion of the range of *M. f. piceus* lies within the Sonoran Desert, but it also extends into the Mohave Desert in Mohave County. The Sonoran Desert is a complex grouping of several, more or less distinct, biotic communities. These include the paloverde-sahuaro (*Cercidium-Cereus*) community, the creosote-bur sage (*Larrea-Franseria*) community, and the saltbush (*Atriplex*) community (Lowe, 1964). The Sonoran Desert is the hottest and the lowest in elevation of the four North American deserts. The Mohave Desert includes creosotebush, Joshua-tree, blackbush, and saltbush as principal association-types. There is a striking paucity of desert trees and the Mohave Desert is essentially transitional between the warmer, lower Sonoran Desert to the south and the cooler, higher Great Basin Desert to the north (Lowe, 1964). Lowe (1964) noted that it ranges to approximately 4,500 ft in elevation.

In California *M. f. piceus* occurs in the Lower Colorado Valley section of the Sonoran Desert (Shreve and Wiggins, 1964), east of the Peninsular Ranges and the Mohave Desert in San Bernardino and Inyo counties. In addition, the range of *piceus* extends into the Chaparral and Coastal Sagebrush vegetation of the Peninsular and Transverse Mountain ranges. In the Death Valley of Inyo County, Turner and Wauer (1963) found *piceus* to be "the most common snake of the Valley oases . . . It occurs about the mesquite and tamarisk groves . . . and frequents the washes and canyons and the open sage flats below the pinyon-juniper association." In the area around Indian Wells, Riverside County, Mosauer (1935) found *piceus* "in the dune region" and "in the sand hills."

The red racer also extends into the Great

Basin Desert in southern and western Nevada and in extreme southwestern Utah.

The subspecies *M. f. ruddocki* is confined to the Central Valley of California, occurring in both the San Joaquin and Sacramento portions. Brattstrom and Warren (1953) stated that "the dominant vegetation is grassland or Oak-Savannah," and Shelford (1963) reported that the primary original vegetation was composed of various species of grasses in bunch form (bunch-grass grassland). Much of the Central Valley is now under cultivation, which may account for the apparent scarcity of *ruddocki*; this seems also to be the case with *Crotaphytus wislizenii silus*, another valley endemic (Montanucci, 1965).

In Baja California *Masticophis flagellum* is found in all the major phytogeographic areas of the peninsula. *M. f. piceus* is found in that section of the Lower Colorado Valley desert that extends into Baja California, east of the San Pedro Mártir Mountains, about as far south as Bahía de Los Angeles. This area is characterized by a simplicity of floral elements. *Larrea tridentata* and *Franseria dumosa* (burweed) are dominant shrubs (Shreve and Wiggins, 1964).

The major portion of the range of *M. f. fuliginosus* lies within the boundaries of the Sonoran Desert in Baja California, but it also extends into the California phytogeographic area (chaparral and sclerophyll woodland) and the Cape Region phytogeographic area (Wiggins, 1960; Shelford, 1963). The latter area is one in which the vegetation is similar to that of the tropical scrub lowlands of Sinaloa (West, 1964). A number of tropical deciduous plants of mainland affinity occur in this region. The other Baja California subdivisions of the Sonoran Desert in which *M. f. fuliginosus* occurs include the Vizcaino Region, the Central Gulf Coast, and the Magdalena Region. The Vizcaino Region is distinctive because of the presence of several leaf-succulent plants. The Central Gulf Coast flora is dominated by sarcocaulous trees of the genera *Bursera* and *Jatropha*, which have trunks of an exaggerated diameter. The Magdalena Region is characterized by a shared dominance of trees and large succulents (cacti) (Shreve and Wiggins, 1964). Linsdale (1932) mentioned that a speci-

men of the black phase of *fuliginosus* was "shot while lying in the sun at the edge of brush on a sandy bank near a marsh" and a specimen of the light phase was "found among rocks" at Comandú and another was "found under a low bush on the desert" on Isla Santa Magdalena. Leviton and Banta (1964) saw two specimens that were "very active on the leeward side of sand dunes" at Bahía de Los Muertos and 4.9 miles SE Pescadero. Another was found coiled up inside a cardón log.

Etheridge (1961) reported collecting one specimen on Isla Cerralvo and seeing others in the high, rolling sand dunes at the southern end of the island.

In Sonora, *M. f. piceus* is found in the Gran Desierto and is apparently restricted to it, although there are no records between the road from Sonoita and Punta Peñansco, and from along the road from Desemboque to Nogales. The distribution of *M. f. cingulum* in Sonora is mainly within the limits of the Sonoran Desert (Shreve and Wiggins, 1964). The range also extends somewhat farther north and east into the area around Cananea, and farther south into the thorn forest of southern Sonora. The distribution of *M. f. cingulum* to the east is effectively limited by the pine-oak woodland and, at higher elevations, the coniferous forests of the Sierra Madre Occidental. *M. f. cingulum* is completely isolated along the greater part of its eastern range limits from *M. f. lineatus* to the east (there is almost certainly some contact between *cingulum* and *lineatus* in the area to the north of the main ranges of the Sierra Madre Occidental, e.g., in the low areas between the Sierra Pulpito and Sierra de San Luis; however, no specimens are available from this area).

Within the Sonoran Desert, *M. f. cingulum* is found in all subdivisions. It occurs in the Lower Colorado Valley, the Arizona Upland, the Plains of Sonora, an area of transition between the very arid type of desert vegetation to the north and the more humid subtropical thorn forest vegetation typical of west coast Mexico, the Central Gulf Coast, an area very similar in vegetational characteristics to that of the eastern coast of Baja California below Bahía de Los Angeles, and the Foothills of Sonora, a fairly rugged area with elements of both the des-

ert vegetation and the thorn forest vegetation (Shreve and Wiggins, 1964).

The distribution of *Masticophis flagellum* in Sinaloa is apparently limited to the thorn forest of the northern portion of the state; the vegetation of the area around El Dorado, the southernmost locality for *Masticophis flagellum* in the Pacific coastal lowlands of Mexico, is described by Fugler and Dixon (1961) as being originally composed of "a heavy forest of mixed native hard- and softwoods." They further stated that "the heavy clayish soils, not utilized for agriculture, bear typical desert vegetation, such as saguaro, yucca, sparse brush of various types, and desert softwoods." The southward dispersal of *Masticophis flagellum* in this region would seem to be limited by the appearance of elements of the tropical lowland vegetation in central Sinaloa.

SUMMARY AND CONCLUSIONS

The generic name *Masticophis* is used for the whipsnakes instead of the taxonomically unstable name *Coluber*. *Masticophis mentovarius* is not considered to be close to the basic stock from which the *flagellum* group arose, but rather to be an advanced form that has the fourth and fifth supralabials fused into a single scale.

Color pattern proved to be the most taxonomically useful character complex; the most important aspects are summarized below. *Masticophis flagellum flagellum* has two adult pattern types, a pale tan pattern resembling that of the juvenile of that subspecies, and a more typical pattern that is dark brown anteriorly and ran posteriorly. The extent of dark brown pigment on the anterior portion of the body and the coloration of the posterior portion of the body are geographically variable, specimens from the southeastern portions of the range being paler than specimens from the northwestern portions of the range.

Masticophis flagellum testaceus has two types of ground color and three types of color pattern. One ground color is pink or red, this phase characterizing three disjunct populations in Trans-Pecos Texas, eastern New Mexico, and eastern Colorado. A ran ground color is found throughout the remainder of the range of the subspecies. The three types of color pattern (a unicolor dor-

sum, a narrow-banded dorsum, and a wide-banded dorsum) occur throughout the range of *M. f. testaceus*.

Masticophis flagellum lineatus is one of two subspecies that shows little pattern variability. Intergradation between *M. f. lineatus* and *M. f. testaceus*, and between *M. f. lineatus*, *M. f. piceus*, and *M. f. cingulum* takes place over a large area in western New Mexico and southeastern Arizona, respectively.

Masticophis flagellum piceus has two phases, one black, the other red. The black phase occurs in south-central Arizona and is most common within a 20-mile radius of Tucson, Pima County.

Masticophis flagellum ruddocki is the other subspecies that shows little pattern variability. Intergradation between *M. f. ruddocki* and *M. f. piceus* occurs in low montane passes at the southern end of the San Joaquin Valley.

Masticophis flagellum cingulum, as envisioned in this study, has a range that encompasses all of Sonora, with the exception of the Gran Desierto of the northwestern portion of the state, and extreme south-central Arizona. This subspecies exhibits considerable variation in color pattern, ranging from a banded phase to one in which the dorsum is uniformly black or red. These pattern changes are clinal in nature.

The subspecies name *Masticophis flagellum fuliginosus*, a new combination, is applied to the form inhabiting the peninsula of Baja California. This subspecies has a pale and a dark phase, each of which exhibits variability in both color and pattern. The two phases occur on the islands on both sides of the peninsula.

A distinctive, but poorly known, pattern variant occurs in northern Sinaloa.

Ventrals and subcaudals exhibit both geographic and individual variation. The subcaudals also are subject to sexual dimorphism to a slight degree. The scale reduction pattern exhibits considerable individual variation, but certain aspects appear to have geographic significance. Only individual variation is exhibited by the head scutellation.

ACKNOWLEDGMENTS

During the course of this study I have been aided by a number of people who have lent me

specimens or who have provided me with information or advice. First of all, I would like to thank my former major professor, Dr. Douglas A. Rossman, who has always encouraged my research on this and other topics and given freely of his advice. I should like also to thank the other members of my committee, Dr. George H. Lowery, Dr. J. Harvey Roberts, Dr. Albert H. Meier, and Dr. Walter J. Harman.

To the following people I would like to extend my sincere gratitude for their patience with my requests for the loan of large numbers of a very large snake and/or information or advice: Steven C. Anderson, Walter Auffenberg, Richard J. Baldauf, Charles M. Bogert, W. Glen Bradley, Bryce C. Brown, E. Milby Burton, Francis M. Bush, Janalee P. Caldwell, William J. Cliburn, Joseph F. Copp, Peter Diekiewicz, William G. Degenhardt, James R. Dixon, Charles L. Douglas, Neill H. Douglas, William E. Duellman, Harold A. Dundee, B. Gandy, Glenn Gentry, Bryan P. Glass, Harvey L. Gunderson, Donald E. Hahn, M. Max Hensley, M. B. Keasey, III, Edmund D. Keiser, C. A. Ketchersid, John P. Kerr, F. Wayne King, John M. Legler, Alan E. Leviton, Ernest A. Liner, Charles H. Lowe, Jr., Edmond V. Malnate, T. Paul Maslin, Clarence J. McCoy, John S. Mecham, John D. Miller, Robert H. Mount, Michael M. Ovchynnyk, William M. Palmer, James A. Peters, Neil D. Richmond, Douglas A. Rossman, Norton M. Rubenstein, Allan J. Sloan, Hobart M. Smith, Henry M. Stephenson, Wilmer W. Tanner, Ray C. Telfair, III, Robert A. Thomas, Donald W. Tinkle, Charles F. Walker, Ernest E. Williams, Kenneth L. Williams, and John W. Wright.

I would also like to thank the following individuals for contributing information useful in this study: Andrew Arata, Ralph W. Axtell, Joseph R. Bailey, C. L. Baker, Rollin H. Baker, Roger W. Barbour, Albert P. Blair, H. T. Boschung, Jr., James L. Christiansen, Joseph T. Collins, James Dobie, Arthur C. Echternacht, Richard Etheridge, Denzel E. Ferguson, T. P. Haines, Laurence M. Hardy, Robert F. Inger, James C. List, Wilfred T. Neill, Brent B. Nickol, Kenneth S. Norris, Gerald C. Raun, R. J. Robel, James T. Tanner, and Richard Thomas.

I want sincerely to thank Howard W. Campbell, Joseph F. Copp, and my former fellow graduate students, Richard M. Blaney, Donald E. Hahn, Edmund D. Keiser, R. Earl Olson, Gerald C. Schaefer, and Kenneth L. Williams, for giving freely of their knowledge concerning whipsnakes.

I would also like to thank Mr. and Mrs. Roger Conant for the use of two photographs from their joint photographic collection and Richard M. Blaney, William G. Degenhardt, Howard K. Gloyd, Gerald C. Schaefer, and Robert G. Webb for the use of photographs from their respective collections.

I am grateful to the late Laurence M. Klauber for the loan of a large amount of data compiled by him during his study of western *Masticophis flagellum*.

My sincere thanks go to Anthony W. Romano and Robert M. Stabler for the gift of specimens.

Finally, I wish to thank Patricia Blaney who typed large portions of the final dissertation copy and Richard M. Blaney who is responsible for the reproduction of many of the photographs.

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TULANE STUDIES IN ZOOLOGY AND BOTANY

Volume 16, Number 3

May 6, 1970

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INTRODUCED GULF COAST MOLLUSCS

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TYPE SPECIMENS OF FISHES IN THE TULANE UNIVERSITY COLLECTION WITH A BRIEF HISTORY OF THE COLLECTION

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TULANE UNIVERSITY
NEW ORLEANS

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INTRODUCED GULF COAST MOLLUSCS

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ABSTRACT

Of the ten species of molluscs which are known to have been introduced into the Gulf Coast area of the United States, four have been studied over a five year period; two of these, *Bradybaena similaris* (Ferussac) and *Lamellaxis gracilis* (Hutton), were given concentrated attention; the other two, *Rumina decollata* (Linnaeus) and *Gulella bicolor* (Gould), while not studied as intensively, were used for comparative purposes. Study of dispersal since introduction showed that these animals are still spreading. The means of dispersal appears to be through man's activities relating to the transport of plants. Studies of biological requirements and tolerances by the snails indicate that they are well adapted to the types of habitats found in this area. Life history and ecological data reveal that further spread is likely.

INTRODUCTION

Some members of the gastropod fauna of the United States are not native. They have been introduced in various ways to our shores from other land masses. Such biological introductions often pose problems in the control of the immigrant species, largely because we have no knowledge of rates, and in many cases the means, of the distribution or changes of ecological tolerances on the part of the introduced organisms.

The goal of this study was to take a segment of an introduced fauna and try to determine from whence it came, when and how it was introduced, and the rate and means of dispersal since being introduced. It was proposed also to study some of the ecological factors influencing the distribution of these introduced species, including a morphologi-

cal study. Data gathered in this latter study will be published separately.

The reported introduced fauna of the Gulf Coast study area (Houston, Texas to Mobile, Alabama: Figure 1), at the inception of this study numbered ten species. From these, four were selected for the purpose of study. They were chosen on the bases of availability and ease of raising in the laboratory. Two of them, *Lamellaxis gracilis* (Hutton) and *Bradybaena similaris* (Ferussac), were selected for intensive study while the others, *Gulella bicolor* (Gould) and *Rumina decollata* (Linnaeus), were examined more casually. The reason for limiting the study to these four was simply a matter of keeping the work involved within reasonable limits.

PROCEDURAL METHODS

Effecting the proposed study resulted in dividing it into several phases:

1. Points of Origin; When and How Introduced

This phase of the project dealt largely with the correlation of past and present molluscan distributions with ship routes, cargoes, and currents. It involved literature searches and discussions with port authorities and shipping companies. It was necessary here to become acquainted and maintain contact with the members of the United States Department of Agriculture Quarantine Division.

2. Rate and Means of Dispersal

This phase of the study consisted of making collections of these animals throughout the Gulf Coastal study area

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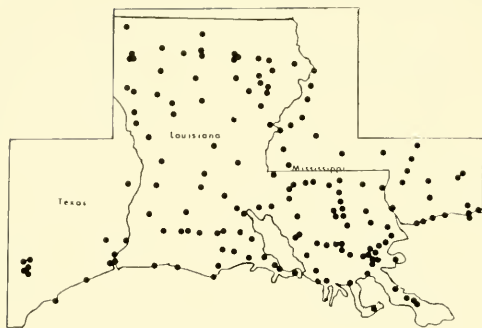


Figure 1. The study area. From Houston, Texas to Mobile, Alabama and northward to the level of the northern border of Louisiana. Dots indicate collection sites.

to determine present distributions (Figure 1) and the making of several follow-up collections to determine if further dispersal is occurring at present. Correlated with this phase of the study were visits to major United States collections to check further on distributions. Determining *means* of dispersal proved to be a difficult task. Involved in this was the questioning of individuals such as nurserymen, gardeners, and so forth and it was not always easy to obtain accurate answers. Sometimes these individuals became suspicious that we might somehow be accusing them of wrong-doing in having these animals and they would then become defensive and not give complete answers. Most, however, were very helpful. Careful surveys of all nurseries and greenhouses in New Orleans and Baton Rouge were made to determine what introduced species were there (Dundee and Watt, 1962; Hermann, Strickland and Dundee, 1965). Time limitations made it necessary to concentrate detailed studies of this phase at the Port of New Orleans.

3. Habits of Introduced Molluscs

It was also necessary to study in detail the habits of the molluscs both in field and laboratory. Laboratory colonies were begun in 1959 and from then through 1967, there were only brief periods when we were without colonies of these animals. Data on food habits, reproductive habits, longevity, variability, ecological tolerances,

and life histories, were gathered from these laboratory colonies.

Colonies were easily maintained in the laboratory. Clear plastic containers of various sizes were used. Into each was put a layer of sand with a piece of paper toweling over part of it. The containers were kept damp with rap water in an air-conditioned room where the temperature ranged between 22–25°C and the relative humidity near 40 percent. The significant humidities in the containers were much higher but no special check of them was made in routine daily care. One side of the room, which had an eastern exposure, contained large glass windows, hence the animals were regularly exposed to daylight. Food consisted of head lettuce leaves. The containers were cleaned and the toweling replaced at least every other day.

Simultaneously, similar data were gathered from field stations for each of these species. In addition, marking of field individuals with nail polish gave some information on rates of movement.

ACKNOWLEDGMENTS

This work was made possible through United States Public Health Service research grant GM-07194. I extend my sincere appreciation to that organization.

I am also indebted to my various student assistants: Mrs. Patti Watt Hermann, Mr. Baldwin Shields Stutts, Mr. John Deris, and Mrs. Dian Hitt Sanders. All of them have been of much help.

My husband, Dr. Harold A. Dundee, has accompanied me on many of the field trips and has helped make many of the collections. To him I owe sincere thanks.

FINDINGS

1. *Points of Origin; When and How Introduced*

This discussion will be based entirely upon the Port of New Orleans. Of necessity, the discussion of introductions must be speculative since there is no record of the actual moment and method of introduction.

The first recorded use of the port was in 1699 with the first settlements in the area of present-day New Orleans (Sinclair, 1942).

TABLE 1. Point of origin of each species of mollusc and its distribution in the period 1699–1905.

SPECIES	ENDEMIC TO:	DISTRIBUTION DURING PERIOD
<i>Bradybaena similaris</i> (Ferrusac)	Southeast Asia	Brazil, W. Indies, Hawaii, Mauritius
<i>Lamellaxis gracilis</i> (Hutton)	Tropical Americas	Tropics of world; Mobile, 1885 (Binney)
<i>Gulella bicolor</i> (Gould)	India, southeast Asia	Tropics of world; W. Indies, Cuba, S. America
<i>Rumina decollata</i> (Linnaeus)	Mediterranean area: S. France, Italy, Sicily, Canary Islands	In Bermuda and Havana (Smith, 1912); in Philadelphia 1897 (Johnson, 1900)

Thus we know that these species must have been introduced after that time. The first record of each of them in the New Orleans area is as follows:

<i>Bradybaena similaris</i> (Ferussac)	1939	<i>Gulella bicolor</i> (Gould) was observed about 1940 by Dr. H. Harry (personal communication) but was not reported. Knowing when the port was first used and the first recorded date of the animals in the city sets the time of introduction of these species. If one now determines the point of origin of each of the species and the distribution at the turn of the 18th century as shown in Table 1, one then can compare those geographical positions with points of origins of cargoes inbound to New Orleans (Table 2)
(Harry, 1948)		
<i>Lamellaxis gracilis</i> (Hutton)	1905	
(Pilsbry, 1946)		
<i>Gulella bicolor</i> (Gould)	1958	
(Dundee, 1961)		
<i>Rumina decollata</i> (Linnaeus)	1906	
(Pilsbry, 1946)		

TABLE 2. Brief history of the Port of New Orleans.

DATE	IMPORTS	ORIGIN OF IMPORTS
1699	Provisions	France
1710	Provisions, brandy, tobacco	Cuba, Santa Domingo, Martinique, W. Florida
1710	Furs	Ohio Valley
1718	FOUNDING OF NEW ORLEANS	
1720	Slaves	West Africa
1763–1776	Powder, lead, clothing	Great Britain
1803	Provisions, first coffee	France, Spain, Brazil
LOUISIANA PURCHASE—MANY PEOPLE MOVING IN		
1806–1813	Various items pirated from Spanish ships and smuggled into the port	Spain
1812	FIRST REGULAR STEAMBOAT FROM NATCHEZ, MISSISSIPPI	
1812–1862	Wines, brandies, cutlery, tools, China, cotton goods, sugar, rum, coffee, fruits, mahogany, rosewood, silver, cochineal, pimento	France Great Britain, Cuba and the islands
1862	BLOCKADE OF THE PORT. No imports except cotton, sugar, and rice.	
1862	QUARANTINE OF PORT AGAINST YELLOW FEVER	
1865	ALL CIVIL WAR RESTRICTIONS REMOVED. MANY NEW SHIPPING LINES ESTABLISHED	
1871	FIRST RAILROAD	
1874	Bananas	Colon, Ecuador, Honduras, Guatemala, Costa Rica
1899	Tropical fruits	United Fruit Company established
Late 1800's	Rubber, palm kernels, sisal, hardwoods	W. Coast Africa, Belgian Congo

TABLE 3. United States Department of Agriculture interceptions of molluscs during 1959 and 1960 in New Orleans (Morris, 1959, 1960).

GENUS	CARGO	POINT OF ORIGIN
<i>Bulinulus corneus</i> (Sowerby)	Bananas	Ecuador
<i>Chilina</i> cf. <i>fluminea</i> (Maton)	Plant	Brazil
<i>Cochlicella barbara</i> (Linnaeus)	General cargo	France, N. Africa
<i>Helicella</i> (4 spp.)	General cargo	France, Greece, N. Africa
<i>Limax marginatus</i> Müller	Cut flowers	Guatemala
<i>Solaropsis monile</i> (Broderip)	Bananas	Ecuador
<i>Succinea</i> sp.	General cargo	N. Africa
<i>Theba pisana</i> (Müller)	General cargo	N. Africa, Italy, France
<i>Zonitoides arboreus</i> (Say)	Orchid	Philippines

and arrive at a logical conclusion as to approximate time and means of introduction. These animals are assumed to have arrived by ship, since New Orleans was surrounded by a swampy wilderness divided by a network of waterways. Road and railroad travel were limited until much later (Civil War period). The first railroad travel was available in the 1870s. Even as late as the early 1800s overland travel by means other than railroad was practically non-existent thus negating the likelihood that snails were brought in from Mexico and/or Central America overland.

Table 2 summarizes the history of the Port of New Orleans in relation to this discussion.

Since 1865 many ships have included New Orleans on their regular itineraries. Some of those arriving from endemic areas for these snails carry cargoes which are likely ones for harboring such animals.

Actual interceptions of molluscs by the Quarantine Division, United States Department of Agriculture in New Orleans in several recent years point out the potential for molluscan introductions. For example, in relation to this present problem, in 1960 one of the interceptions at the Port of New Orleans was *Lamellaxis mauritanus* (Pfeiffer) on an orchid from Venezuela (Morris, 1960). Table 3 summarizes several such interceptions during the years 1959, 1960. Studies on other molluscs have also revealed that they too are arriving in this country on imported materials and it would seem that nursery stocks provide an ideal method of entry. Inspections will not reveal each single individual which might be hidden on the plant parts or the ova which might be in the soil around the roots of the plants.

It rapidly became obvious that these animals are arriving through man's activities rather than being passively carried on float-

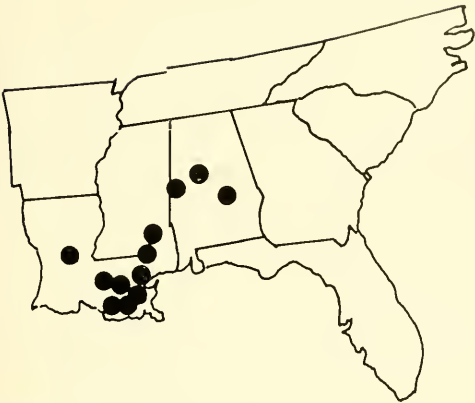
ing vegetation or the like. Also, it is obvious that most of the introductions are accidental even though there have been cases where individuals have brought snails from another country to use as food items here. Many of these "foreign" snails can be bought alive in the markets of our country as food items (Figure 2). The question then becomes: what is to prevent them from crawling out of the container and establishing a colony? It is my belief that that is exactly how species such as *Helix aspersa* Müller and others originally were established in the port area of New Orleans.

2. Rate of Dispersal

All four of the migrants with which this paper is concerned are widely distributed in the warm areas of the world at the present time. Within the United States both *Bradybaena similis* and *Rumina decollata* seem to be pushing northward as evidenced by our collections. Figure 3 shows the present known distribution of *B. similis* while



Figure 2. Snails for sale. *Helix aspersa* at 35¢, and *Otala lactea* at 75¢.



BRADYBAENA SIMILARIS

Figure 3. Present distribution of *Bradybaena similaris* in the United States.

Figure 6 gives that of *R. decollata*. *Gulella bicolor* (Figure 4) by contrast, still seems to be confined to the area where it was introduced—at least here in the Gulf Coast area. *Lamellaxis* (Figure 5), at first glance, would seem to be widely distributed in the eastern half of the United States; however, most of the northern records are greenhouse localities.

Within the designated study area *Bradybaena* and *Lamellaxis* are both slowly widening their distribution as shown by our repeated collections of the area (Figures 7 and 8). When this study began in 1959, *B. similaris* seemed to be limited to the New Orleans-to-Baton Rouge and Mobile areas.



GULELLA BICOLOR

Figure 4. Present distribution of *Gulella bicolor* in the United States.

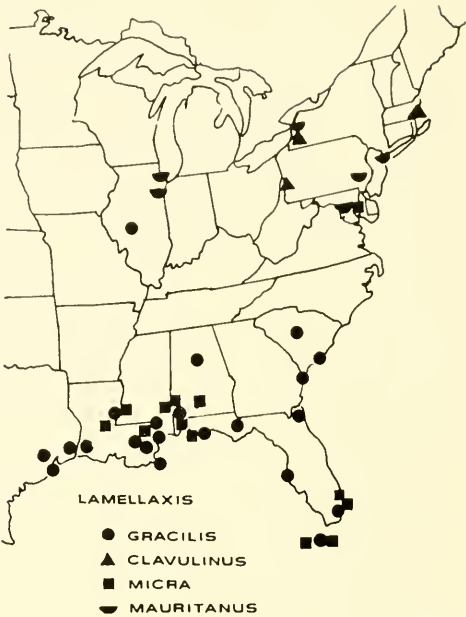


Figure 5. Present distribution of *Lamellaxis* in the United States.

By 1961 we found it on the Mississippi Gulf Coast, spreading northeastward into southwestern Mississippi and northward to Alexandria, Louisiana. By 1962 it had been introduced to Hammond, Louisiana on the north and to Houma and Jeanerette on the south, and towards the mouth of the Mississippi River on the southeast. In 1964 it had moved into Thibodaux, Louisiana on the southeast. Complete further checks have not



Figure 6. Present distribution of *Rumina decollata* in the United States.

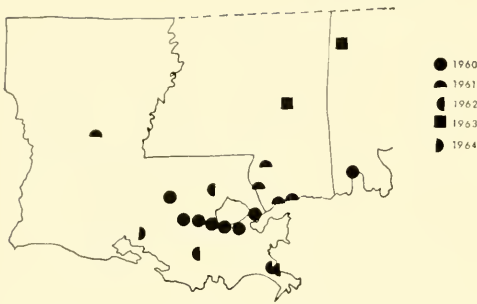


Figure 7. Study area distribution of *Bradybaena similaris* showing dispersal over a 5-year period.



Figure 8. Study area distribution of *Lamellaxis gracilis* showing dispersal over a 5-year period. Explanation as for Figure 7.

been made since; however, plans are to survey again soon.

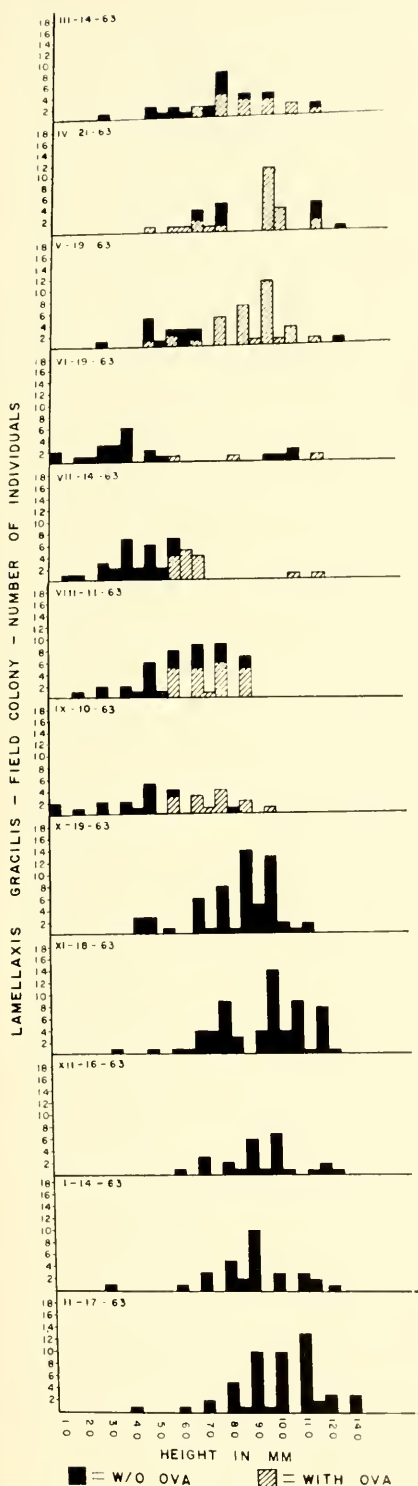
Lamellaxis gracilis distribution has also been carefully observed over a five year period (Figure 8). By 1959 and 1960, *L. gracilis* seemed to be limited to New Orleans, Baton Rouge, Biloxi, Houston, and Beaumont. In 1961 we found it spreading from the Biloxi locality into neighboring Gulfport, Moss Point, and Pass Christian in Mississippi. At the same time it was found in Picayune and Hattiesburg, Mississippi, probably originating from New Orleans. The year 1962 found it established to the south of New Orleans in four localities and in one more to the north. By 1963 it had managed to extend about 200 miles further north into Natchez, Mississippi and Natchitoches, Louisiana. In 1964 it was still pushing westward from New Orleans along the lower half of the state. More recent findings show it in Pensacola, Florida on the east and Lake Charles, Louisiana and Galveston, Texas on the west.

3. Means of Dispersal

There are two ways in which land molluscs are distributed: actively by their own movement, and passively by being transported by other organisms or the environment. Doubtlessly most of the distribution of molluscs which we see today can be accounted for by the activity of the molluscs themselves over millions of years. However, with the numerous forms of transportation of modern man, many molluscs such as those involved in this work find themselves in areas far from their native habitats. Such introductions often pose severe problems in the control of intro-

duced species. With the absence of natural population checks (predators, diseases, and the like), the immigrant is free to "run wild" biologically until a balance is again established in the ecosystem.

The questions often asked are these. How are these organisms being transported? Why are we unable to stop introductions? Answers, of course, vary with the organisms in question. It has become increasingly obvious during this study that the four mollusc species herein considered are being transported through the movements of plant materials. This is being further borne out by another study on introduced slugs now in progress. It was also found to be true in New York state (Karlin and Naegele, 1960). We first suspected this in noticing that these molluscs were always found in association with man's activities—in cultivated areas, near import centers, and so forth. Never have we found them away from man's activity areas even though habitats elsewhere appear to be satisfactory. If then we were correct that these snails were moving about as passengers on vegetation, where would be the most likely spots to find them? In gardens, public and private. In cemeteries. In nurseries and greenhouses. Private gardens were ruled out immediately as a study source because of the problems associated with entering such property. Checking public gardens and cemeteries resulted in finding many new localities for the snails. If we could find the same snails in greenhouses, we could reasonably assume that they got there with the plants (as opposed to riding on bird feet, drifting on floating materials and so on). Such examinations did reveal the snails in many cases.



It also revealed other molluscs not previously reported from the area.

Our next question was that of why it is that these snails are not discovered and killed. Many discussions with owners and operators of nurseries and greenhouses made us aware that there is a constant battle between man and snail. All owners and operators use some type of molluscicide and are constantly trying to prevent plant damage from these animals. It also became obvious that, despite the fact that they wish to rid themselves of such pests, they are not thorough enough. We were able to find many molluscs under the tables where nothing economically important was being grown and where they are not using the chemicals. It was difficult to find snails on the about-to-be-sold plants, however. How then, were these snails being distributed? Our studies have revealed that they spread largely through transport of snail ova which have been deposited in the soil around the plants.

4. Future Dispersal

If, in the five years of studies, these snails have spread considerably through much of the study area, what then of the future? How far can they go? Baker (1958: 143) summarizes it well: "In time, dispersal means that each species would occur everywhere unless it be stopped by barriers . . ." Basically there are two types of barriers which prevent an organism from spreading everywhere: physical (geographical) and ecological. Since we have already established in this particular case that physical barriers are easily spanned with the aid of man, the immediate question becomes: Are there any ecological barriers which will stop the spread of these animals? Can they exist wherever man takes them? To answer these questions it was first necessary to determine something of the biology of the animals.

A. Life History: *Lamellaxis gracilis*.

In Figure 9 one can see that, in the New Orleans area, the reproductive season is initiated in mid-March at which time ova may be seen through the shell. This situation prevails to late May at which time the ova are deposited. Young of various ages are present

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Figure 9. Field colony, *Lamellaxis gracilis*.

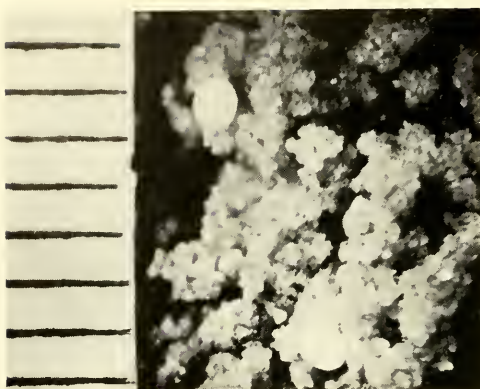


Figure 10. Ova in soil, *Lamellaxis gracilis*.

from early June through the summer (Figure 9). By about October they have grown to approximately 4–5 mm in height. Early October is another period of ova deposition followed by some young overwintering in the 3 mm stage.

Laboratory colonies maintained for over a year tend to behave in a somewhat different manner in that March to June is a period of ova production and is followed by an interval of no ova nor young and then by another peak of production of ova in late summer followed by constant low ova production for the rest of the year. This is most likely the result of the colony being in a more or less constant temperature-humidity atmosphere (temperatures from 22–25°C and relative humidities constantly in the 40 percent range).

The maximum number of ova ever seen in one snail was 10; the average number per gravid snail was 5 seen at one time. However, based on laboratory experiments, the average number of ova deposited per snail per breeding season is 79. In lab colonies 55 percent of the ova hatched. These ova (Figure 10) of *Lamellaxis gracilis* are almost spherical, white, have "hard shells," and are deposited singly in the surface of the soil, but not covered by soil. There appears to be no effort at "nest building"; the ova are simply placed individually in the soil; usually several ova will be found together as a clutch.

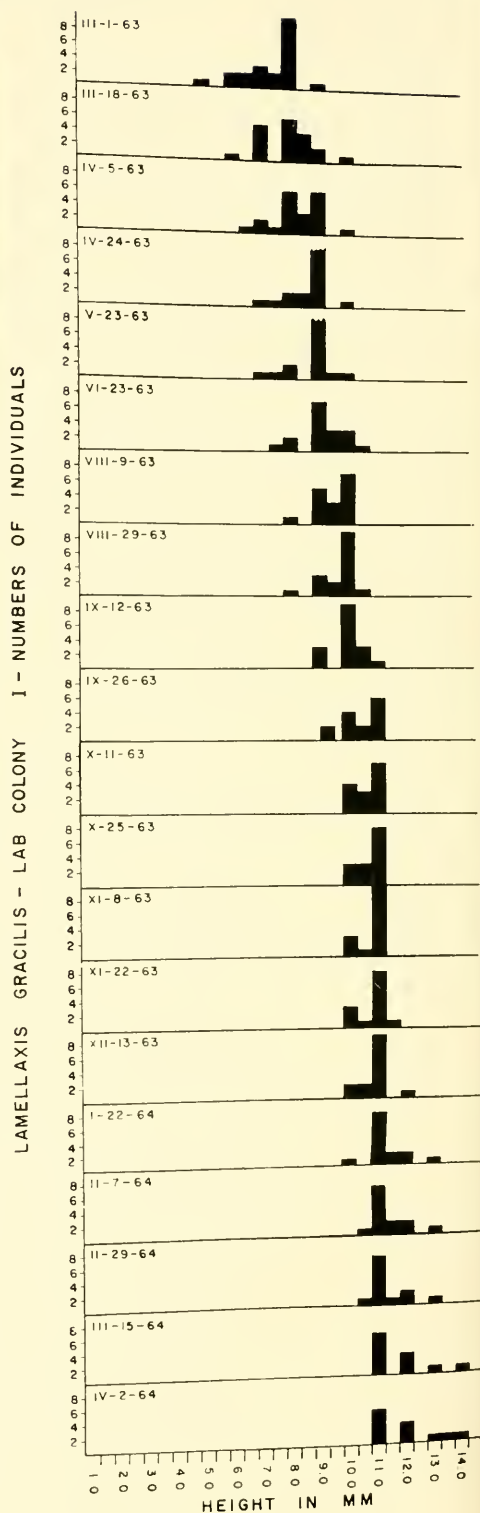


Figure 11. Laboratory, *Lamellaxis gracilis*. Colony begun with 21 individuals and all ova and/or young removed from it regularly.

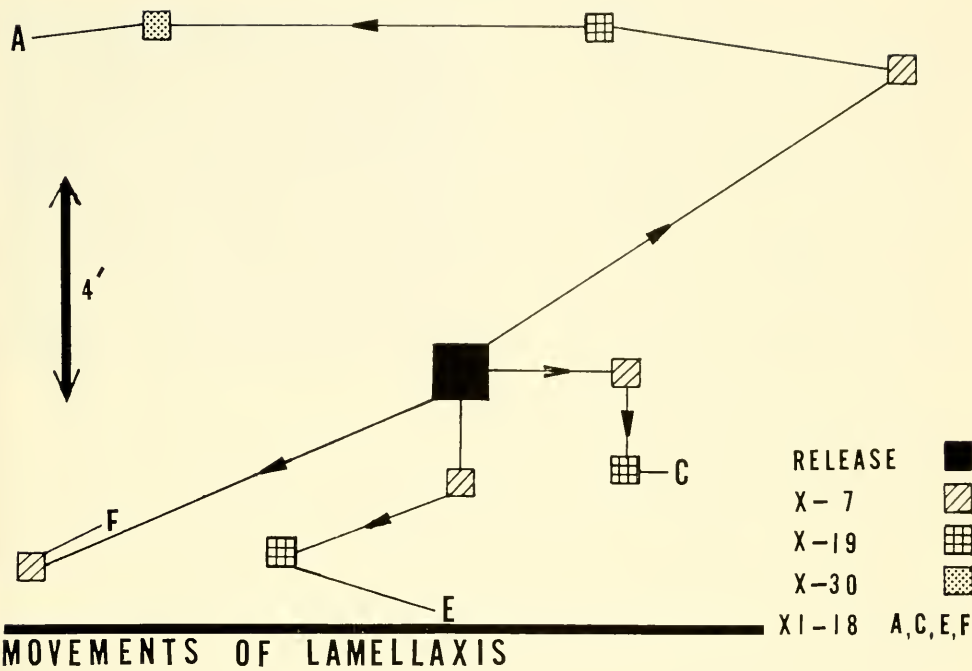


Figure 12. Movements of marked individuals, *Lamellaxis gracilis*.

These ova are small enough (0.5–0.9 mm in diameter) to be easily overlooked by individuals transporting plant materials.

Incubation time in nature is approximately 10 days. However, on 2 occasions in the laboratory incubation was completed in 7 days. *Lamellaxis micra*, by contrast, had an incubation time of 15 days in the laboratory. Its ova are similar but smaller.

Lamellaxis gracilis growth rate is approximately 1 mm/month. Those young which hatch in mid-June are in the 5 mm class by late October to early November. This rapid growth rate then seems to slow with a continued constant, gradual growth until death. Figure 11 shows a laboratory colony which was begun with 21 adults of various sizes. Constant removal of all ova and/or young immediately upon discovery kept this colony intact for over a year. During that time 10 individuals died and the remaining 11 continued growth as shown on the histogram.

Adult *Lamellaxis gracilis* (as evidenced by the initiation of reproductive cycles) range in size from 4–14 mm in height and have whorl numbers between 5.5–10. Individuals exceeding 12 mm in height are rare. *Lamel-*

laxis micra adults range in size between 4.5 and 7.2 mm in height.

The life span of an individual *L. gracilis* appears to be approximately one year with some apparently surviving through most of the second year. These observations need substantiation since it was impossible to obtain recapture of marked individuals after a lengthy period.

B. Habitat and Habits: *Lamellaxis gracilis*.

These snails are found in areas of man's activities—in particular, in areas where man has been active and then has allowed the area to stand idle for a period. A prerequisite is cover of some sort—boards, bricks, leaves, or other objects which can provide shelter. The snails are always under these objects during periods of dryness. After rains they are easily available crawling about on the surface. At no time are they more than 1.3 cm or so above ground. As cooler weather arrives, *Lamellaxis gracilis* descends into the soil. During one period of -5°C , the animals were found 7.6 cm down in the soil. During a January period when the soil temperature stayed close to 8°C , the snails, despite heavy

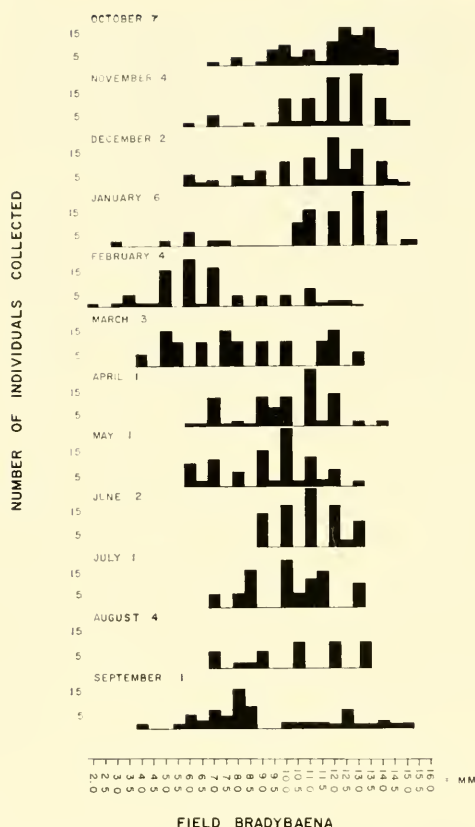


Figure 13. Field colony, *Bradybaena similis*.

rains, remained from 2.5–7.6 cm below the surface. Even at these depths individuals are grouped together; for example, in a 4.5×10 cm area 27 individuals were found 1.3 cm down in the soil. Under the circumstances described in this paragraph the individuals are lying dormant (hibernation?).

Feeding experiments were run in the laboratory. Individuals were offered plant parts of each of the species of plants found in the habitat. Results indicated that they will feed readily on leaves of *Laportea canadense*, *Panicum* sp., and *Crepis* sp. Other plants from the habitat were not acceptable. Karlin's (1956) assumption was that since *Lamellaxis* and two other species were never found more than an inch above soil surface, they were feeding "only on plant matter in the mulch. . ." The observation of the closeness to the soil is in accordance with our findings; however, it seems likely that these snails do

use the leaf matter described above in their normal living but probably rely on those leaves which drop off or are low down. In the laboratory any of the species of *Lamellaxis* seem to survive for long periods on nothing more than lettuce leaves.

Repeated marking experiments all met with failure. One is shown in Figure 12. Here 6 snails were marked differentially with nail polish and released as indicated on October 1. One week later we were unable to find 2 of them (B, D). By a month and a half later (November 18) the other 4 were in the positions shown. With the advent of colder weather shortly thereafter, we were unable to get further recaptures of these. It is believed, however, that enough other recaptures were made—albeit not after lengthy periods—to state tentatively that *L. gracilis* seems to remain within 10 ft or less of its point of release; whether this is true during the entire life is unknown.

C. Life History: *Bradybaena similis*.

In the New Orleans area *B. similis* deposits its ova in January and by early February many young snails are present (Figure 13). The older members of the colony appear to die off soon after the winter season as shown in Figure 13. Through spring and summer the young are growing and a middle-aged group is present. Again in late July there is a brief period of egg deposition so that by mid-August to early September there are again a few young present in the population. In this area these young reach a subadult stage before cooler weather occurs. Just as with *Lamellaxis* the laboratory colonies continue producing ova and young throughout the year in small numbers.

Bradybaena ova (Figure 14) by contrast with those of *Lamellaxis*, are clear and gelatinous when first deposited. They are frequently stuck together (probably accidentally) and always laid as a cluster. The adult usually makes a concavity in which the ova are placed; they are not covered with soil. Each ovum is spherical and measures approximately 2 mm in diameter. In laboratory colonies the average number of ova per snail per breeding season was 38.

Incubation time in the lab was 11 days and in the field it ranged from 10–15 days.

The smallest *Bradybaena similis* at hatching measure 1 mm in height, 1.75 mm in

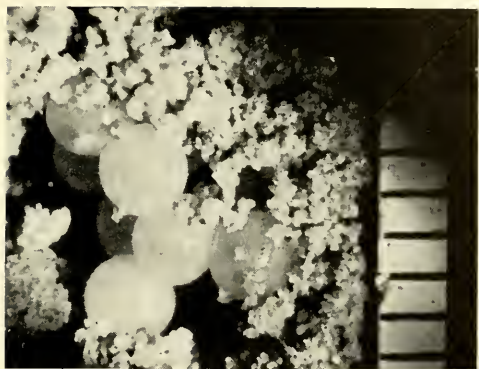


Figure 14. Ova in soil, *Bradybaena similaris*.

diameter, and have 1.75 whorls. Six months later most of these had reached 3.25 mm in height, 5.25 mm in diameter, had 3.5 whorls, were sexually mature and reproducing. All newly hatched young were without color bands which are characteristic of 91.1% of the population here. The bands began to show by the time the snail had reached 2 mm diameter and 1.5 mm in height. Of the 1566 *Bradybaena similaris* checked, 3.9% had no bands at all in the adult and 6% showed only very faint banding. The remainder have a characteristic light yellowish shell with a brown band. This stands in contrast to the same species in Japan (Komai and Emura, 1955) where there are 4 distinct genetic types: the 2 mentioned above plus brown forms with and without bands. Why these introduced forms lack the brown phases is not known at this time.

Adult *Bradybaena similis* in this area also differ much in size from those reported by Komai and Emura (1955). They report them to be "18 mm in diameter and 12 mm in height at most of its size." The tallest *Bradybaena* we have recorded in many measurements is 11 mm and the one of greatest diameter was 15.5 mm. These are rare. This smaller size, plus the absence of the two color phases, suggests that some factor in the habitat, present in Japan but missing here, is exerting a considerable influence on these snails. We plan to do some follow-up work on this phase.

D. Habitat and Habits: *Bradybaena similis*.

It has been suggested that this species is closely associated with sugar cane (Pilsbry,

Hyatt and Cook, 1912). While we have found it in close proximity to sugar cane fields here, it is not necessarily associated with them. Many of the colonies are found living in various types of tall grasses in vacant lots, along railroad tracks, and so forth. Others, however, have become established in gardens. Sugar cane was introduced from Santo Domingo to this area between 1771 and 1775 in Jesuit Bend, a community 15 miles south of New Orleans. Since *B. similis* was known from the West Indies at that time (Table 1), it is quite probable that it was introduced here with the sugar cane.

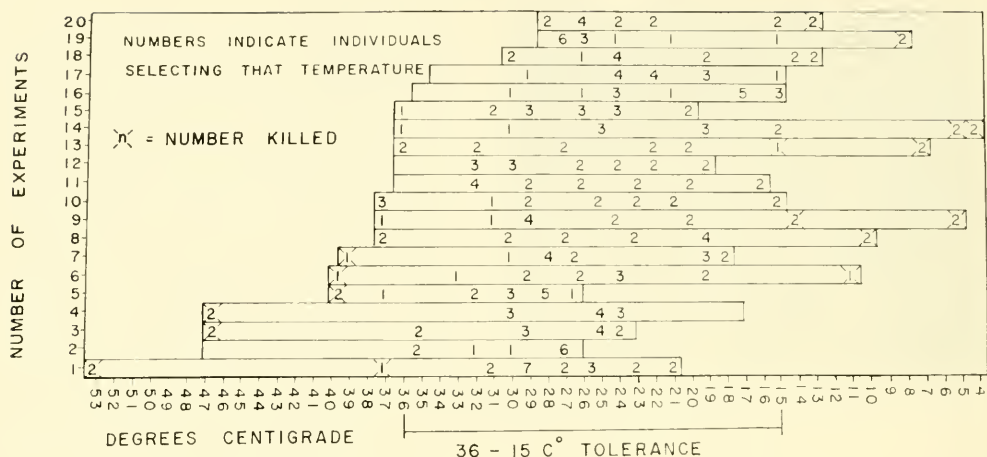
In feeding experiments we were unable to get *B. similis* to eat anything but monocots and, in particular, the grass, *Panicum brachyanthus* and a lily, *Lilium canadense*. All of the plants from their normal habitats were offered.

These snails are much less secretive than *Lamellaxis*. They are just as likely to be found out in the open (either active or dormant) as under objects. Occasionally they are seen a few feet high on vegetation or on the sides of vertical objects. Usually they are not found over 15 cm above the ground on the plants. Most often they are seen at night crawling about on grass which previously has fallen down and dried. Often hundreds of them can be seen in this type of situation.

Marking experiments in 3 different localities revealed that individuals move little at any time. The maximum distance traveled away from one point of release by any one individual was just under 3 m in a 2 month period. This, of course, is not taking into consideration how much movement occurred within the 3 m radius during that period by this individual. Marking was done with nail polish; this seems to lead to an early death in the snails.

E. Ecological Tolerances.

(1) Temperature: An experimental device similar to, and patterned after, that used by Dainton (1954) was used to determine temperature tolerances of these snails. This device consists of a trough in which a temperature gradient can be maintained. Different ranges can be had by using different water temperatures at the inputs. Snails are introduced throughout the length of the



LAMELLAXIS GRACILIS TEMPERATURE SELECTION

Figure 15. Temperature selections, *Lamellaxis gracilis*.

trough and allowed a period in which to select the temperature most suitable for them. The results are recorded after 30 minutes. After repeated trials for each species, during which the temperature ranges were varied (Figure 15) so as to include all reasonably possible temperatures, it was found that the range of tolerance for *Lamellaxis gracilis* is 15–37°C while that for *Bradybaena similis* is slightly greater: 12–38°C. Interpretations of these data must be made in conjunction with other factors. If one were to use only these temperature data, one would be forced to conclude that these snails can live nowhere in the United States except Florida; as has already been shown (Figures 3 and 5) the snails *do* live elsewhere. If one plots upon the present distribution picture the average minimum temperature for January, one finds that these snails, which, according to our experimental data can tolerate no less than 12°C, are living in areas where the average January minimum is 6°C. Here again, it is of interest to note that Komai and Emura (1955) found that –7°C for an hour or 2 killed nearly all adults; perhaps these snails are able to tolerate much lower temperatures in their native homeland. When one considers that these snails protect themselves from the cold as described above, then it is not too surprising to find them living in colder areas than the laboratory experiments indicate are possible. During the period in

which we were recording soil temperatures, the lowest reading was a December one of –2°C at a 3 inch soil depth. The snails at this level were aggregated and they had their epiphragms in position, but many of them were dead. This was true for both *Lamellaxis* and *Bradybaena*.

The upper limits of tolerance of these snails are such that they should be able to tolerate temperatures anywhere in the United States since the highest average July temperature falls easily within their range of tolerance. The maximum could be withstood through the use of shelter.

(2) Desiccation: Experiments consisted of merely placing the snails in dry bowls (one per bowl) at room temperature (23–29°C) and humidity (40%) and examining them at intervals to see if they were still alive. It was found that dead ones could be easily identified by shining a narrow beam from a spot lamp through the shell and looking to see if the animal was intact. Surprising differences in tolerances to desiccation were revealed in our experiments. In several hundred trials, the time which *Bradybaena* was able to remain alive ranged from 30–217 days with an average time of death being 122 days, or approximately 4 months. In contrast, the maximum time which *Lamellaxis* was able to remain alive was 121 hours, or approximately 5 days. To evaluate these data one must keep in mind that the 40% relative

TABLE 4. Molluscan associates of the introduced species.

SPECIES	STATION 1	STATION 2	STATION 3	STATION 4
<i>Bradybaena similaris</i>		X	X	X
<i>Gulella bicolor</i>		X	X	X
<i>Rumina decollata</i>		X		
<i>Lamellaxis gracilis</i>	X	X	X	X
<i>Helicina orbiculata</i>	X	X		X
<i>Polygyra texasiana</i>		X	X	X
<i>Retinella indentata</i>	X	X		
<i>Hawaiiia miniscula</i>		X	X	X
<i>Pupoides marginatus</i>			X	X
<i>Polygyra septemvolva</i>		X		X
<i>Praticolella griseola</i>		X		X
<i>Mesodon perigraptus</i>		X		
<i>Strobilops texasiana</i>		X		
<i>Deroceras laeve</i>		X		

humidity found in the lab during these experiments is low in contrast to that in the environment in this Gulf Coast area and the microenvironment of these snails. Thus, the animals should be able to withstand periods of drought longer in nature than they can in the laboratory. The fact that 3 of the 4 species treated here can survive adverse conditions for long periods of time through estivation is doubtlessly of high survival value. It is of interest that *Lamellaxis gracilis*, despite the fact that it is widely distributed over the world now, does not have this ability. Obviously, a combination of other factors has overcome this one factor which would appear to be a distinct handicap to an introduced species.

Similar experiments with *Rumina decollata* and *Gulella bicolor* revealed that under the circumstances described some individuals of both species are able to survive at least 7 months. One *Gulella* was still alive at the end of 214 days. Rascop (1960) found that relative humidity below 15% and a temperature above 85°F (29°C) caused *Rumina* to estivate. Further, Rascop found that snails estivating at room temperature for 8 months lost an average of 55.56% of their body weight.

(3) Soil pH: Throughout our studies we found pH ranges at the various study stations of 6.4–7.1 for both *Lamellaxis gracilis* and *Bradybaena similaris*. Karlin (1956) concluded that pH could not be considered a critical factor in greenhouses since the mean pH where *L. gracilis* and others lived was 5.9. He pointed out that while it is well-known that snails are scarce on acid soils,

other factors such as the addition of gypsum and the presence of other minerals compensated for the low pH.

(4) Moisture: None of these 4 snails is associated with visible moisture in the form of swampy or marshy conditions. All live in well-drained areas. Among the 4, they could be ranked on the basis of 5 years of observation both in the field and in the lab, according to their moisture tolerances (from wettest to driest): *Lamellaxis*, *Bradybaena*, *Gulella*, *Rumina*. Observations lead us to believe that moisture, in the form of relative humidity, is of far more direct importance to the land mollusc than standing or falling water. Relative humidities of 85% and up are not uncommon in this area even in the day. A dry day would have a humidity in the 40% range. From this standpoint, then, conditions in this Gulf Coast area seem to be ideal for these snails.

(5) Relative Population Densities: *L. gracilis* and *B. similaris* are, in the habitats described, extremely abundant. One can easily collect hundreds of specimens within half an hour. The habitats, however, are frequently widely separated so that this heavy abundance actually forms a spotty type of distribution. Some populations were large enough that we were able to remove 50 or more individuals every two weeks without any noticeable change in the numbers present. In contrast, *Gulella bicolor* and *Rumina decollata* are abundant nowhere in this area. The distribution is not only spotty but within a given habitat one would be likely to find no more than 10 individuals in the half-hour period.

(6) Associates: Table 4 reveals that there are no associates which are always found with a given introduced species. The most common joint occurrence is that of the two introduced species, *B. similaris* and *L. gracilis*. Apparently no significance may be attached to the presence of any of the molluscan associates of these introduced snails.

Other associates such as ants (Formicidae) do seem to be extremely significant to the well-being of these snails, however. Ants are very common in this entire study area. We observed repeatedly that whenever ants invaded a habitat such as the area beneath a large boulder it would not be long before the snails would all be dead. We do not know the reason. We did run several simple experiments of enclosing the snails and the ants in gallon jars together and again the results were the same—the snails soon died (controls did not). This, perhaps, might be investigated further with a view towards biological control if such is ever needed.

5. Economic Considerations

Fortunately, at the present time, none of the introduced molluscs in the Gulf Coast area have become severe pests under natural conditions. Even though they are a problem in greenhouses and nurseries, this is a different matter. *B. similaris* is an annoyance in a few flower gardens, but no more so than endemic species such as *Mesodon thyroideus*. In any event, no serious damages to crops nor any nuisance from numbers of snails such as was the case with *Achatina fulica* (Mead, 1961) has occurred in this area.

DISCUSSION

We can, after examining the foregoing data, return to the question posed in the beginning of section 4 of this paper: Can these snails (in particular, *B. similaris* and *L. gracilis*) exist wherever man takes them? The general answer, of course, is no. There are many areas, however, where they do not now exist but where they could easily survive. There is no cause to think that they will not spread further northward, eastward, and westward. They should be able to live throughout the lower half of the United States from southern Pennsylvania, the lower half of Ohio, Indiana, and Illinois, southern Missouri and Kansas, southeastern Colorado and along the entire west coast. The average

winter minimum temperatures of this area are no less than -2°C (28.4°F). Since we are considering only average temperatures the snails in the northernmost part of this area would have to remain confined to sheltered type habitats and, therefore, should be much more spotty in distribution than elsewhere.

Drier parts of this range, namely in west Texas, New Mexico, Arizona, and southern California should act as barriers to the general spread in that direction. However, again, cultivated areas should provide habitats which have adequate moisture to maintain high enough relative humidities in the micro-habitats, especially for small snails such as *Lamellaxis*.

Through follow-ups on this study we will know definitely whether, by a brief survey of such factors as have been dealt with in this paper, one would be able to predict the future dispersal of an introduced land mollusc. It seems now that such will be the case.

It appears that most of the introduced snails which do become established do not become agricultural pests. Of the 10 species which are known to have been introduced in the New Orleans area at the inception of this study, 4 have failed to become established, 4, as shown in this paper, are still spreading, and 2 other species are also established and spreading. None of these has yet become a real pest to agriculture or horticulture.

It appears also that preventing the entrance of these foreign invaders into this country is impossible. The United States Department of Agriculture is doing an admirable job of keeping down the numbers entering but even they are not preventing the entrance of many. As long as we import materials we will accidentally import snails. One of the best sources of foreign land molluscs in this country is the nursery. It is ideal for their reception, maintenance, and distribution.

The key to whether or not one of these immigrants will become a severe pest seems to lie in its food habits and its reproductive potential, assuming of course that it is able to find a suitable habitat. It appears that if an investigation of a species' reproductive and food habits were undertaken as soon as an introduced land mollusc is discovered, it should be easily possible to predict whether the immigrant would become a severe agri-

cultural pest; if so, immediate control measures could be instituted.

Perhaps such a program could be undertaken by the United States Department of Agriculture through a program which would encourage malacologists and other interested biologists to be on the alert for new introductions in their areas. If and when such is found the ideal situation would be for the United States Department of Agriculture to request that a study be made by a malacologist, supported by U.S.D.A., to determine if the immigrant is likely to become a pest. If chances are good, then control action could be initiated promptly; if not, there would no longer be a need for constant vigil at our ports for that species.

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TYPE SPECIMENS OF FISHES IN THE TULANE UNIVERSITY COLLECTION WITH A BRIEF HISTORY OF THE COLLECTION^{1,2}

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INTRODUCTION

A brief history of the Tulane University fish collection and a list of type specimens are given in this paper. The publication of the latter is recognized as part of the University's responsibility following the recommendations of the International Code of Zoological Nomenclature (Recommendation 72 D. Institutional responsibility) 1961. Formerly, some paratypes were housed elsewhere (as noted) but were acquired by Tulane on a gift basis. All types are grouped in a separate room apart from the rest of the general collection. Jars containing holotypes are encircled with red paint and those containing paratypes are similarly marked with blue paint. The types as well as the general collection specimens are arranged by families in a phylogenetic sequence following Berg's (1947) classification system. Within the family the genera and species are arranged alphabetically. Each label bears a family number which has been derived by a renumbering of Berg's families of fishes which contain living representatives, that is, families with only fossil forms were excluded because fossil fish material is kept separate from extant material.

HISTORY OF THE TULANE UNIVERSITY FISH COLLECTION

During the latter half of the last century Tulane University had an active exhibit museum which included an array of natural history items as well as art items, minerals, and so forth. In the early 1950's when the old museum was disbanded there were only a few fish specimens remaining and these were suspended by thread in formalin. None had labels and so the several dozen specimens were discarded. Two dry-mounted fish speci-

mens, a cotton stuffed *Acipenser fulvescens* which has "Niagara Falls, July 1881" printed on its ventral side a partial skin of a *Rachycentron canadus* which has "New Orleans, June 3, 1894" written on the exposed part of the artificial wooden body are the only specimens retained from the former Tulane Museum collection of fishes.

The author started the modern Tulane University fish collection in the fall of 1950. However, it was not until July 11, 1951, that the first entry was made in a permanent catalog. The collection has grown steadily and at present, December 31, 1969, there are 60,030 catalog entries which total 1,849,315 specimens. Some of the earlier series, 1951 to about 1955, were stored in 70% ethanol, but the bulk of the specimens have been stored in 40% isopropyl alcohol, which is the currently used storage fluid. Of the two percentages of isopropyl alcohol available commercially (99% and 91%) 99% is used for dilution to 40% with ordinary tap water.

The fish skeletal collection totals 549 specimens, most of which are complete skeletons. The dry fish skeletal material and the cleared and alizarin-stained, glycerin stored specimens are cataloged separately from the above mentioned alcohol stored material. Moreover, the 953 x-ray negatives are cataloged separately on 4 × 6 file cards. The 953 x-rays represent a total of 12,042 specimens.

The Tulane University fish collection is not a typological or local reference collection. Geographically the Tulane collection has excellent representation of southeastern, southern and southwestern United States fresh water fishes and good representation of central United States, Mexican, Central American (particularly Costa Rica) fresh water fishes and marine fishes from the Gulf of Mexico and Caribbean Sea.

During the entire two decade period the author has been the curator of the fish collection. During the first decade of history a number of students helped in curating the collection, in particular, Sue Whitsell (Fingerman), Myrna Andersson (Wilkens) and

¹ Contribution Number 1 from the Laboratory of Systematic and Environmental Biology, Environmental Science Center, Tulane University.

² Published by Tulane University in fulfillment of an institutional responsibility recommended by the International Commission on Zoological Nomenclature, with partial financial support from the Louisiana Research Foundation.

Bangalore I. Sundararaj. In 1963 John S. Ramsey became the first volunteer student curator, followed by Clyde D. Barbour and Glenn H. Clemmer. Ramsey organized the type material; sorted, identified and cataloged a vast amount of material; studied and identified most of the unidentified cataloged material that had accumulated up to that time and took care of most of the loan requests during the 1963 to 1965 period.

Dr. D. E. Copeland (then Chairman of the Zoology Department) was instrumental in obtaining the first curatorial staff appointment for the fish collection. Mr. Albert Harris was appointed as assistant to the curator of fishes in 1965. Upon his resignation in 1966, Mr. Frank Thomas became the assistant to the curator and has continued in this position to the present time.

Without the staff appointment the ever increasing requests for loans would have been an overburdening task for the curator. Needless to say the growth of the collection and the production of publications would have been greatly curtailed without the assistant. Too, during the two decade period parts of the collection have been moved several times from one building to another on different sides of the campus and at the present time we are in the process of moving the entire collection to the Environmental Science Center which is 15 miles away on the west bank of the Mississippi River.

LIST OF TYPE SPECIMENS OF FISHES IN THE
TULANE UNIVERSITY LABORATORY OF
SYSTEMATIC AND ENVIRONMENTAL
BIOLOGY*

Clupeidae

Brevoortia gunteri Hildebrand, 1948, Smithsonian Misc. Coll. 107 (18):1-39, 9 figs.

Paratype: TU10792 (formerly United States National Museum No. 129802, sent to Tulane University as gift exchange on January 5, 1954), Texas, Aransas County, Aransas Bay, collected by Gordon Gunter.

Alepisauridae

Alepisaurus brevirostris Gibbs 1960, Breviora, Mus. Comp. Zool., (123):1-14.

* The formal opening of the Laboratory of Systematic and Environmental Biology will be announced during the latter part of 1970 or early 1971.

Paratype: TU 22990, Atlantic Ocean, latitude 37° 44' north, longitude 65° 42' west, 1957, collected by M. V. Delaware.

Cyprinidae

Algansea monticola Barbour and Contreras, 1968, Proc. Biol. Soc. Wash., 81:101-108.

Holotype: TU 40869, from Mexico, Zacatecas, Rio Juchipila near town of Jalpa, at Highway 70 bridge, one mile east of the intersection with Highway 41, 30 June 1963, CDB 63-27, collected by Clyde B. Barbour and Salvador Contreras.

Paratypes: TU30611, 49 specimens from same collection as holotype; TU30608, 76 specimens, from Mexico, Zacatecas, Rio Juchipila at Mal Paso (a little walled town) about 16 miles east of Ciudad Garcia Salinas, 28 June 1963, CDB 63-23, collected by Barbour and Contreras; TU 30609, 131 specimens, from Mexico, Zacatecas, tributary to Rio Juchipila, about 5 miles south of Villanueva on Highway 41, 28 June 1963, CDB 63-24, collected by Barbour and Contreras; TU 30610, 18 specimens from Mexico, Zacatecas, Rio Juchipila at Tabasco, upstream of bridge at south end of town, 29 June 1963, CDB 63-25, collected by Barbour and Contreras.

Nocomis effusus Lachner and Jenkins 1967, Copeia, 1967 (3):557-580.

Paratypes: TU 19488, 2 specimens from Tennessee, Rutherford County, Stones River, 6.5 miles north of Murfreesboro, Highway 231, 7 September 1958, RDS 2758, collected by Suttkus and Myrna Andersson; TU 32838, 5 specimens from Tennessee, Fentress County, tributary to Wolf River, 9.8 miles north of Jamestown, Highway 127, 3 June 1964, RDS 3474, collected by Suttkus and John S. Ramsey; TU 33115, 2 specimens from Tennessee, Cheatham County, Harpeth River, 8 miles east of White Bluff, Highway 70, 15 July 1964, JSR 64-60, collected by Ramsey and Dan W. Walton; TU 33125, 11 specimens from Tennessee, Williamson County, South Harpeth River, 4.2 miles east of Fairview, Highway 96, 15 July 1964, JSR 64-61, collected by Ramsey and Walton; TU 33171, 21 specimens from Tennessee, Rutherford County, West Fork Stones River at west edge of Murfreesboro, Highway 96, 15 July

1964, JSR 64-63, collected by Ramsey and Walton; TU 33194, 1 specimen from Tennessee, Rutherford County, Stones River at south limit of Walterhill, Highway 231, 16 July 1964, JSR 64-64, collected by Ramsey and Walton.

Notropis asperifrons Suttkus and Raney, 1955, Tulane Stud. Zool., 3(1):1-33.

Paratypes: TU 2974, 22 specimens from Alabama, Wilcox County, Gravel Creek tributary to Pursley Creek 6.3 miles south of Camden, Highway 11, 3 June 1951, RDS 2140, collected by Royal D. Suttkus and Charles D. Hancock; TU 3063, 5 specimens from Alabama, Wilcox County, tributary to Pursley Creek, 1.8 miles east of Camden, Highway 10, 3 June 1951, RDS 2138, collected by Suttkus and Hancock; TU 3426, 8 specimens from Alabama, Wilcox County, Pursley Creek, tributary to Alabama River, 3.4 miles southwest of Camden, Highway 11, 3 June 1951, RDS 2139, collected by Suttkus and Hancock; TU 4251, 28 specimens from Alabama, Shelby County, tributary to Waxahatchee Creek, 4.7 miles southwest of Columbia on Highway 25, 15 June 1952, RHG 356, collected by Robert H. Gibbs, Jr. and Philip P. Caswell.

Notropis baileyi Suttkus and Raney, 1955, Tulane Stud. Zool., 2(5):69-86.

Paratypes: TU 2637, 29 specimens from Alabama, Monroe County, tributary to Alabama River, 17.3 miles south of Camden, Highway 11, 3 June 1951, RDS 2141, collected by Suttkus and Hancock; TU 2965, 4 specimens from Alabama, Wilcox County, Gravel Creek, tributary to Pursley Creek, 6.3 miles south of Camden, Highway 11, 3 June 1951, RDS 2140, collected by Suttkus and Hancock; TU 3066, 41 specimens from Alabama, Wilcox County, tributary to Pursley Creek, 1.8 miles east of Camden, Highway 10, 3 June 1951, RDS 2138, collected by Suttkus and Hancock; TU 3195, 4 specimens from Alabama, Butler County, Pine Barren Creek, 2.5 miles south of Forest Home, 2 June 1951, RDS 2136, collected by Suttkus and Hancock; TU 3430, 75 specimens from Alabama, Wilcox County, Pursley Creek, tributary to Alabama River, 3.4 miles southwest of Camden, Highway 11, 3 June 1951, RDS 2139, collected by Suttkus and Hancock.

Notropis edwardraneyi Suttkus and Clemmer, 1968, Tulane Stud. Zool. and Bot., 15(1):18-39.

Holotype: TU 49485, from Alabama, Wilcox County, Alabama River at Yellow Jacket Bar, river mile 129.8, 8 March 1967, RDS 4097, Suttkus and Gerald E. Gunning.

Paratypes: TU 44028, 7324 specimens taken with holotype; TU 33381, 1613 specimens from Alabama, Dallas County, Alabama River at Watts Bar, 3.5 miles upstream from Cahaba, River Mile 204.5, 29 June 1964, RDS 3515, Suttkus and Environmental Biology Class; TU 35243, 236 specimens from Alabama, Dallas County, Alabama River at old ferry landing across river from Cahaba, 27-28 June 1964, RDS 3508, Suttkus and Environmental Biology Class; TU 35269, 314 specimens from Alabama, Dallas County, Alabama River at Cahaba where Cahaba River enters Alabama River, 28 June 1964, RDS 3513, Suttkus, Glenn H. Clemmer, James D. Archer and John Van Conner; TU 35323, 28 specimens from Alabama, Clarke County, Alabama River along left bank across river from Choctaw Bluff, 2 July 1964, RDS 3519, collected by Suttkus and Environmental Biology Class; TU 40293, 297 specimens from Alabama, Wilcox County, Alabama River at Evans Upper Bar, River Mile 135.8, 7 April 1966, RDS 3857, collected by Suttkus and Gunning; TU 40303, 1020 specimens from Alabama, Wilcox County, Alabama River at Yellow Jacket Bar, River Mile 129.8, 7 April 1966, RDS 3858, collected by Suttkus and Gunning; TU 40320, 491 specimens from Alabama, Wilcox County, Alabama River at Tait Bar, River Mile 122.4, 7 April 1966, RDS 3859, collected by Suttkus and Gunning; TU 40335, 243 specimens from Alabama, Wilcox County, Alabama River at Wilcox Bar, River Mile 120.3, 7 April 1966, RDS 3860, collected by Suttkus and Gunning; TU 40900, 289 specimens from Alabama, Wilcox County, Alabama River at Evans Upper Bar, River Mile 135.8, 28 June 1966, RDS 3918, collected by Suttkus, Gunning and Clemmer; TU 40925, 85 specimens from Alabama, Wilcox County, Alabama River at Yellow Jacket Bar, River Mile 129.8, 28 June 1966, RDS 3919, collected by Suttkus, Gunning and Clemmer; TU 40940, 226 specimens from Alabama, Wilcox County, Alabama River at Tait Bar, River Mile 122.4, 28

June 1966, RDS 3920, collected by Suttkus, Gunning and Clemmer; TU 40950, 109 specimens from Alabama, Wilcox County, Alabama River at Wilcox Bar, River Mile 120.3, 29 June 1966, RDS 3921, collected by Suttkus, Gunning and Clemmer; TU 41400, 390 specimens from Alabama, Wilcox County, Alabama River at Yellow Jacket Bar, River Mile 129.8, 4.6 miles east of Yellow Bluff Post Office, 1 July 1966, RDS 3924, collected by Suttkus and Environmental Biology Class; TU 41608, 284 specimens from Alabama, Wilcox County, Alabama River at Evans Upper Bar, River Mile 135.8, 4 October 1966, RDS 4011, collected by Suttkus and Gunning; TU 41618, 33 specimens from Alabama, Wilcox County, Alabama River at Yellow Jacket Bar, River Mile 129.7, 4 October 1966, RDS 4012, collected by Suttkus and Gunning; TU 41632, 92 specimens from Alabama, Wilcox County, Alabama River at Reeves Bar, River Mile 128.5, 4 October 1966, RDS 4013, collected by Suttkus and Gunning, TU 41639, 187 specimens from Alabama, Wilcox County, Alabama River at Tait Bar, River Mile 122.5, 4 October 1966, RDS 4014, collected by Suttkus and Gunning; TU 41655, 119 specimens from Alabama, Wilcox County, Alabama River at Wilcox Bar, River Mile 120.5, 5 October 1966, RDS 4015, collected by Suttkus and Gunning; TU 41666, 147 specimens from Alabama, Wilcox County, Alabama River at Ohio Bar, River Mile 111.6, 5 October 1966, RDS 4016, collected by Suttkus and Gunning; TU 41670, 301 specimens from Alabama, Monroe County, Alabama River at Stein Island, River Mile 107.5, 5 October 1966, RDS 4017, collected by Suttkus and Gunning; TU 41695, 83 specimens from Alabama, Wilcox County, Alabama River at Evans Upper Bar, River Mile 135.8, 5 August 1966, RDS 3945, collected by Suttkus and Gunning; TU 41711, 29 specimens from Alabama, Wilcox County, Alabama River at Evans Lower Bar, River Mile 133, 5 August 1966, RDS 3946, collected by Suttkus and Gunning; TU 41726, 16 specimens from Alabama, Wilcox County, Alabama River at Yellow Jacket Bar, River Mile 129.7, 5 August 1967, RDS 3948, collected by Suttkus and Gunning; TU 41732, 19 specimens from Alabama, Wilcox County, Alabama River at Reeves Bar, River Mile 128.5, 5 August 1966, RDS

3949, collected by Suttkus and Gunning; TU 41745, 63 specimens from Alabama, Wilcox County, Alabama River at Tait Bar, River Mile 122.5, 5 August 1966, RDS 3950, collected by Suttkus and Gunning; TU 41755, 12 specimens from Alabama, Wilcox County, Alabama River at Wilcox Bar, River Mile 120.5, 5 August 1966, RDS 3951, collected by Suttkus and Gunning; TU 41761, 9 specimens from Alabama, Wilcox County, Alabama River at Ohio Bar, River Mile, 111.6, 5 August 1966, RDS 3952, collected by Suttkus and Gunning; TU 41772, 151 specimens from Alabama, Monroe County, Alabama River at Stein Island, River Mile 107.5, 5 August 1966, RDS 3953, collected by Suttkus and Gunning; TU 41791, 22 specimens from Alabama, Monroe County, Alabama River at St. James Bar, River Mile 104, 5 August 1966, RDS 3954, collected by Suttkus and Gunning; TU 41797, 4 specimens from Alabama, Monroe County, Alabama River, at Bates Bar, River Mile 99, 5 August 1966, RDS 3955, collected by Suttkus and Gunning; TU 41813, 10 specimens from Alabama, Monroe County, Alabama River at Silver Creek Bar, River Mile 87.6, 6 August 1966, RDS 3957, collected by Suttkus and Gunning; TU 41823, 1 specimen from Alabama, Monroe County, Alabama River at mouth of Limestone Creek, River Mile 80.1, 6 August 1966, RDS 3958, collected by Suttkus and Gunning; TU 42731, 370³ specimens from Alabama, Wilcox County, Alabama River at Evans Upper Bar, River Mile 135.8, 19 December 1966, RDS 4065, collected by Suttkus and Gunning; TU 42737, 5630 specimens from Alabama, Wilcox County, Alabama River at Yellow Jacket Bar, River Mile 129.5, 19 December 1966, RDS 4066, collected by Suttkus and Gunning; TU 42746, 687 specimens from Alabama, Wilcox County, Alabama River at Tait Bar, River Mile 122.5, 19 December 1966, RDS 4067, collected by Suttkus and Gunning; TU 42759, 900 specimens from Alabama, Wilcox County, Alabama River at Wilcox Bar, River Mile 120.5, 19–20 December 1966, RDS 4068, collected by Suttkus and Gunning; TU 44011, 175 specimens from Alabama, Wilcox County, Alabama River at Evans Upper Bar, River

³ Given incorrectly in Suttkus and Clemmer, 1968: 10 as 470 specimens.

Mile 135.8, 8 March 1967, RDS 4096, collected by Suttikus and Gunning; TU 44029, 94 specimens from Alabama, Wilcox County, Alabama River at Tait Bar, River Mile 122.5, 9 March 1967, RDS 4098, collected by Suttikus and Gunning; TU 44045, 561⁴ specimens from Alabama, Wilcox County, Alabama River at Wilcox Bar, River Mile 120.5, 9 March 1967, RDS 4099, collected by Suttikus and Gunning; TU 46783, 202 specimens from Alabama, Wilcox County, Alabama River at Evans Upper Bar, River Mile 135.8, 31 May 1967, RDS 4143, collected by Suttikus and Gunning; TU 46796, 395 specimens from Alabama, Wilcox County, Alabama River at bar above Yellow Jacket Bar, 31 May 1967, RDS 4144, collected by Suttikus and Gunning; TU 46802, 223 specimens from Alabama, Wilcox County, Alabama River at Yellow Jacket Bar, River Mile 129.8, 31 May 1967, RDS 4145, collected by Suttikus and Gunning; TU 46819, 43 specimens from Alabama, Wilcox County, Alabama River at Tait Bar, River Mile 122.5, 31 May 1967, RDS 4146, collected by Suttikus and Gunning; TU 46830, 32 specimens from Alabama, Wilcox County, Alabama River at Wilcox Bar, River Mile 120.5, 31 May–1 June 1967, RDS 4147, collected by Suttikus and Gunning; TU 47346, 64 specimens from Alabama, Wilcox County, Alabama River at Evans Upper Bar, River Mile 135.7, 7 August 1967, RDS 4177, collected by Suttikus and Gunning; TU 47361, 49 specimens from Alabama, Wilcox County, Alabama River at Yellow Jacket Bar, River Mile 129.8, 7 August 1967, RDS 4178, collected by Suttikus and Gunning; TU 47374, 86 specimens from Alabama, Wilcox County, Alabama River at Reeves Bar, River Mile 128.5, 7 August 1967, RDS 4179, collected by Suttikus and Gunning; TU 47387, 168 specimens from Alabama, Wilcox County, Alabama River at Tait Bar, River Mile 122.5, 7–8 August 1967, RDS 4180, collected by Suttikus and Gunning; TU 47396, 33 specimens from Alabama, Wilcox County, Alabama River at Wilcox Bar, River Mile 120.6, 8 August 1967, RDS 4181, collected by Suttikus and Gunning; TU 47408, 475 specimens from Alabama, Wilcox County, Alabama River at Ohio Bar, River Mile 111.7,

8 August 1967, RDS 4182, collected by Suttikus, Clemmer and Gunning; TU 47420, 173 specimens from Alabama, Monroe County, Alabama River at Stein Island, River Mile 107.5, 8 August 1967, RDS 4183, collected by Suttikus and Gunning; TU 47435, 229 specimens from Alabama, Monroe County, Alabama River at Bates Bar, River Mile 99.4, RDS 4184, collected by Suttikus and Gunning; TU 47452, 134 specimens from Alabama, Monroe County, Alabama River at Haines Island, River Mile 96, 8 August 1967, RDS 4185, collected by Suttikus and Gunning; TU 47477, 89 specimens from Alabama, Wilcox County, Alabama River at Evans Lower Bar, River Mile 133, 9 August 1967, RDS 4186, collected by Suttikus and Gunning; TU 47491, 24 specimens from Alabama, Monroe County, Alabama River at St. James Bar, River Mile 104, 10 August 1967, RDS 4187, collected by Suttikus and Gunning; TU 47499, 16 specimens from Alabama, Monroe County, Alabama River at Silver Creek Bar, River Mile 87.7, 17 August 1967, RDS 4188, collected by Suttikus and Clemmer; TU 47515, 306 specimens from Alabama, Wilcox County, Alabama River at Hobbs Bar, River Mile 149.5, 18 August 1967, RDS 4189, collected by Suttikus and Clemmer; TU 47762, 143 specimens from Alabama, Wilcox County, Alabama River at Lower Canton Bar, River Mile 156.7, along left bank, 18 August 1967, RDS 4190, collected by Suttikus and Clemmer; TU 47781, 9 specimens from Alabama, Wilcox County, Alabama River at Lower Canton Bar, River Mile 156.7, along right bank, 18 August 1967, RDS 4191, collected by Suttikus and Clemmer; TU 47822, 85 specimens from Alabama, Wilcox County, Alabama River at Hurricane Island, River Mile 166.5, 19 August 1967, RDS 4193, collected by Suttikus and Clemmer; TU 47838, 75 specimens from Alabama, Wilcox County, Alabama River at St. John Bar, River Mile 164.8, 19 August 1967, RDS 4192, collected by Suttikus and Clemmer; TU 47909, 152 specimens from Alabama, Wilcox County, Alabama River at Evans Upper Bar, River Mile 135.7, 26 September 1967, RDS 4204, collected by Gunning and Armand Kuris, TU 47924, 105 specimens from Alabama, Wilcox County, Alabama River at Yellow Jacket Bar, River Mile 129.8, 26 September

⁴ Given incorrectly in Suttikus and Clemmer, 1968: 20 as 461 specimens.

1967, RDS 4203, collected by Suttkus and Clemmer; TU 47936, 39 specimens from Alabama, Wilcox County, Alabama River at Reeves Bar, River Mile 128.5, 26 September 1967, RDS 4204, collected by Suttkus and Clemmer; TU 47968, 230 specimens from Alabama, Wilcox County, Alabama River at Tait Bar, River Mile 122.5, 27 September 1967, RDS 4207, collected by Suttkus and Kuris; TU 47980, 108 specimens from Alabama, Wilcox County, Alabama River at Wilcox Bar, River Mile 120.6, 27 September 1967, RDS 4208, collected by Suttkus and Kuris; TU 47994, 65 specimens from Alabama, Wilcox County, Alabama River at Ohio Bar, River Mile 111.7, 27 September 1967, RDS 4209, collected by Suttkus and Kuris; TU 48012, 232 specimens from Alabama, Monroe County, Alabama River at Stein Island, River Mile 107.5, 27 September 1967, RDS 4210, collected by Suttkus and Clemmer.

Notropis euryzonus Suttkus, 1955, Tulane Stud. Zool., 3(5):83-100.

Paratypes: TU 10700, 8 specimens from Alabama, Russell County, tributary to Little Uchee Creek, 1.1 miles east of Crawford, Highway 80, 17 September 1955, RDS 2520, collected by Suttkus; TU 10718, 60 specimens from Alabama, Russell County, tributary to Uchee Creek, 3.2 miles west of Crawford, Highway 80, 17 September 1955, RDS 2521, collected by Suttkus.

Notropis bypsilepis Suttkus and Raney, 1955, Tulane Stud. Zool., 2(7):159-170.

Paratypes: TU 8883, 4 specimens (formerly part of Cornell University No. 17138) Georgia, Fulton County, Vickery Creek at junction with Chattahoochee River at Roswell, Highway 19, 30 March 1950, ECR 1765 and RDS 1765, collected by Edward C. Raney, Suttkus, C. Richard Robins and Richard Backus.

Notropis imeldae Cortes 1966, An. Esc. nac. Cienc. biol., Mex., 15:185-192.

Paratypes: TU 55375, 5 specimens from Mexico, Oaxaca, Rio Atoyac at Juchatengo, latitude 16° 20' north, longitude 97° 05' west, 16 April 1965, collected by Imelda Martinez and Lauro Gonzalez.

Notropis signipinnis Bailey and Suttkus, 1952, Occ. Pap. Mus. Zool. Univ. Mich., No. 542:1-15.

Paratypes: TU 1133, 164 specimens from Mississippi, George County, Maletts Spring Branch, tributary to Rocky Creek, tributary to Escatawpa River, 6.6 miles southeast of Lucedale, 4 June 1951, RDS 2147, collected by Suttkus and Hancock.

Notropis uranoscopus Suttkus, 1959, Copeia, 1959(1):7-11.

Holotype: TU 15289, from Alabama, Bibb County, Cahaba River, 2.2 miles north of Centerville, 17 March 1957, RDS 2594, collected by Suttkus, Rudolph J. and Helen V. Miller, John DeAbate.

Paratypes: TU 18551, 18 specimens from same collection as holotype; TU 18569, 2 specimens from Alabama, Bibb County, Cahaba River, 2 miles south of Centerville, 5 July 1954, University of Alabama Number 406, collected by Henry Howell, Bryan brothers, Ralph Chermock, A. F. Hemphill, and Herbert Boschung; TU 18570, 8 specimens from Alabama, Bibb County, Cahaba River, 2 miles south of Centerville, 5 July 1954, collected by Jack Mallory; TU 18674, 8 specimens from Alabama, Bibb County, Cahaba River, 8.5 miles north of Centerville, Highway 27 crossing, 8 July 1958, RDS 2738, collected by Suttkus, Myrna Andersson, Susan Salisbury, and John DeAbate; TU 19410, 21 specimens from Alabama, Bibb County, Cahaba River, 8.5 miles north of Centerville, Highway 27 crossing, 8 September 1958, RDS 2760, collected by Suttkus and Myrna Andersson.

Ictaluridae

Ictalurus serracanthus Yerger and Relyea, 1968, Copeia, 1968(2):361-384.

Paratypes: TU 22592, 4 specimens from Florida, Gadsden County, Lake Talquin just west of mouth of Little River, 20 October 1959, JMB 78, collected by James M. Barkuloo, et al.; TU 22642, 1 specimen from Florida, Leon County, Ochlockonee River at Jackson Bluff, Highway 20, 14-15 November 1959, RDS 2861, collected by Suttkus, Barkuloo and Ernest Grover; TU 37226, 3 specimens from Florida, Wakulla County, Sopchoppy River, 2.4 miles south of Sop-

choppy, Highway 319, 27 May 1964, collected by Kenneth Relyea.

Noturus albater, Taylor, 1969, Bull. U. S. Nat. Mus., (282):1-315.

Paratypes: TU 10180, 1 specimen from Arkansas, Newton County, Big Buffalo River, 15.8 miles west of Jasper, Highway 21, 30 April 1955, RDS 2485, collected by Suttkus, Ann Harper, Wanda Hildebrand and Hinton D. Hoese; TU 12240, 15 specimens from Arkansas, Washington County, West Fork White River 6.1 miles south of Fayetteville, Highway 71, 2 September 1955, RDS 2509, collected by Suttkus; TU 12258, 85 specimens from Arkansas, Washington County, White River 8.3 miles east of Springdale, Highway 68, 3 September 1955, RDS 2512, collected by Suttkus; TU 16553, 35 specimens from Arkansas, Washington County, White River 8.3 miles east of Springdale, Highway 68, 4 October 1957, collected by Suttkus, Charles F. Cole, John DeAbate, Susan Harvey, Myrna Andersson, and Bangalore I. Sundararaj; TU 16575, 12 specimens from Arkansas, Washington County, White River 8.3 miles east of Springdale, Highway 68, 5 October 1957, RDS 2667, collected by Suttkus, Cole, DeAbate, Harvey, Andersson, and Sundararaj; TU 22401, 7 specimens from Arkansas, Madison County, War Eagle Creek, 5.4 miles north of Huntsville, Highway 23, 25 October 1959, RDS 2856, collected by Suttkus, Andersson, Sundararaj; TU 22504, 37 specimens from Arkansas, Newton County, Buffalo Fork of White River, 15.5 miles west of Jasper, Highway 74, 24 October 1959, RDS 2853, collected by Suttkus, Andersson, Sundararaj; TU 22514, 2 specimens from Arkansas, Newton County, Buffalo Fork of White River 15.5 miles west of Jasper, Highway 74, 25 October 1959, RDS 2854, collected by Suttkus, Andersson, and Sundararaj; TU 22709, 9 specimens from Arkansas, Cleburne County, Devils Fork Little Red River between Stark and Edgemont, 23 October 1959, RDS 2852, collected by Suttkus, Andersson, and Sundararaj.

Noturus elegans Taylor, 1969, Bull. U. S. Nat. Mus., (282):1-315.

Paratypes: TU 19390, 12 specimens from Kentucky, Green County, Green River 3.8 miles east-northeast of Donnansburg, High-

way 88, 7 September 1958, RDS 2756, collected by Suttkus and Myrna Andersson; TU 19460, 16 specimens from Kentucky, Barren County, tributary to Barren River, 2.6 miles southwest of Lucas, Highway 31E, at old mill dam, 7 September 1958, RDS 2757, collected by Suttkus and Andersson.

Noturus lachneri, Taylor, 1969, Bull. U. S. Nat. Mus., (282):1-315.

Paratypes: TU 7074, 1 specimen from Arkansas, Garland County, 7.7 miles south-southwest of Owensville, 3 miles southeast of U. S. Highway 70, 7 August 1953, EL 94, collected by Ernest Liner; TU 7077, 2 specimens from Arkansas, Garland County, 7.7 miles south-southwest of Owensville, 3 miles southeast of U. S. Highway 70, 7 August 1953, EL 94, collected by Ernest Liner.

Noturus munitus Suttkus and Taylor, 1965, Proc. Biol. Soc. Wash., 78:169-178.

Holotype: TU 26250, from Mississippi, Marion County, Pearl River, 216 miles east of Sandy Hook, 14 November 1955, collected by Suttkus and Kristin T. Nielsen.

Paratypes: TU 11311, 195 specimens from same collection as holotype; TU 1844, 23 specimens from Mississippi, Marion County, Pearl River 2.3 miles east of Sandy Hook, 24-25 November 1951, RDS 2207, collected by Suttkus and Paul K. Anderson; TU 3557, 8 specimens from Mississippi, Marion County, Pearl River, 2.3 miles east of Sandy Hook, 16 February 1952, RDS 2238, collected by Suttkus, Paul K. Anderson, Howard K. Suzuki, Thomas Cain; TU 3627, 73 specimens from Mississippi, Marion County, Pearl River, 4 miles northeast of Sandy Hook, 13 January 1952, RDS 2217, collected by Suttkus, Anderson and Walter D. Stone; TU 3951, 11 specimens from Mississippi, Marion County, tributary to Pearl River, 4.8 miles southeast of Columbia, Highway 13, 23 May 1952, RDS 2297, collected by Suttkus, Cain and Franklin Sogandares-Bernal; TU 4872, 1 specimen from Mississippi, Marion County, tributary to Pearl River, 4.3 miles south of Foxworth, 19 August 1952, RDS 2173, collected by Suttkus, Hancock and Joe Black; TU 7369, 1 specimen from Louisiana, Washington Parish, Pushepatapa Creek, 0.8 mile south of Varnado, 19 January 1952, RDS 2222, collected by Suttkus and Suzuki;

TU 8886, 4 specimens from Mississippi, Marion County, tributary to Pearl River, 0.5 mile south of Hub or 8.5 miles south of Columbia, 28 October 1950, RDS 2013, collected by Suttkus and Clarence Lavett Smith; TU 9709, 3 specimens from Mississippi, Marion County, tributary to Pearl River, 5 miles south of Columbia, 30 June 1954, RDS 2456, collected by Suttkus; TU 10462, 3 specimens from Louisiana, Washington Parish, Pushepatapa Creek, 0.8 mile south of Varnado, 29 June 1954, RDS 2455, collected by Suttkus and Nielsen; TU 11588, 1 specimen from Louisiana, Washington Parish, Pushepatapa Creek, 8.2 miles north of Bogalusa, 7 May 1956, RDS 2556, collected by Suttkus and Field Zoology Class; TU 13954, 214 specimens from Mississippi, Marion County, Pearl River, 2.3 miles east of Sandy Hook, 5 October 1956, RDS 2565, collected by Suttkus, Rudolph J. Miller and Robert K. Chipman; TU 14930, 67 specimens from Mississippi, Marion County, Pearl River, 2.3 miles east of Sandy Hook, 12–13 January 1957, RDS 2576, collected by Suttkus and Miller; TU 14938, 82 specimens from Mississippi, Marion County, Pearl River, 2.6 miles east of Sandy Hook, 6 January 1957, RDS 2574, collected by Suttkus and Miller; TU 15073, 2 specimens from Louisiana, Washington Parish, Pushepatapa Creek, 1 mile south of Varnado or 7 miles north of Bogalusa, 13 January 1957, RDS 2578, collected by Suttkus and Miller; TU 15171, 92 specimens from Mississippi, Marion County, Pearl River, 2.3 miles east of Sandy Hook, 22–23 January 1957, RDS 2580, collected by Suttkus and Norman C. Negus; TU 15465, 2 specimens from Louisiana, Washington Parish, Pushepatapa Creek, 7 miles north of Bogalusa, Highway 21, 21 April 1957, RDS 2600, collected by Suttkus, Robert H. Gibbs, et al.; TU 16148, 6 specimens from Mississippi, Marion County, Ten Mile Creek, tributary to Pearl River, 9.7 miles north of Sandy Hook, 7 August 1957, RDS 2641, collected by Suttkus and Miller; TU 17472, 1 specimen from Louisiana, Washington Parish, Pushepatapa Creek, 0.8 mile south of Varnado, Highway 21, 20 March 1958, RDS 2692, collected by Suttkus, Myrna Andersson and Susan Harvey; TU 17721, 4 specimens from Mississippi, Simpson County, Strong River, 2 miles west of Pinola, 3 April 1958,

RDS 2697, collected by Suttkus, Jayson S. Suttkus and Andersson; TU 17951, 1 specimen from Mississippi, Marion County, Ten Mile Creek, 10.4 miles south of Columbia, Highway 35, 3 May 1958, RDS 2711, collected by Suttkus, Andersson and Sidney Simpson; TU 18739, 2 specimens from Mississippi, Simpson County, Strong River, 2 miles west of Pinola, Highway 28 (formerly Hwy 20), 3 July 1958, RDS 2735, collected by Suttkus, Andersson, and J. S. Suttkus; TU 18963, 60 specimens from Mississippi, Marion County, Pearl River, 2.3 miles east of Sandy Hook, 3 November 1957, RJM 1053, collected by R. J. Miller, Helen V. Miller, Andersson and Donald Boyer; TU 19781, 9 specimens from Mississippi, Simpson County, Strong River, 2 miles west of Pinola, Highway 20, 8 May 1959, RDS 2774, collected by Suttkus and J. S. Suttkus; TU 19825, 52 specimens from Louisiana, Washington Parish, Bogue Chitto River, 1 mile west of Warnerton, 2 May 1959, RDS 2770, Suttkus, Douglas Landwehr, and L. Redman; TU 19880, 3 specimens from Louisiana, Washington Parish, Bogue Chitto River, 1 mile west of Warnerton, 3 May 1959, RDS 2773, Suttkus and Vertebrate Natural History Class; TU 22824, 38 specimens from Mississippi, Marion County, Pearl River, 2.3 miles east of Sandy Hook, 26 October 1959, RDS 2857, collected by Suttkus, Andersson, and Bangalore I. Sundararaj; TU 23127, 1 specimen from Mississippi, Marion County, Pearl River, 2.3 miles east of Sandy Hook, 24 March 1960, RDS 2897, collected by Suttkus and Gerald E. Gunning; TU 23310, 1 specimen from Louisiana, Washington Parish, Bogue Chitto River, 1 mile south of Enon, Highway 437, 3 July 1960, RDS 2913, collected by Suttkus and John S. Ramsey; TU 23351, 1 specimen from Louisiana, Washington Parish, Bogue Chitto River, 2 miles west of Warnerton, Highway 438, 3 July 1960, RDS 2914, collected by Suttkus and Ramsey; TU 23518, 24 specimens from Mississippi, Copiah County, Copiah Creek, 2.4 miles south of Georgetown, Highway 27, 22 July 1960, RDS 2935, collected by Suttkus and Ramsey; TU 23701, 1 specimen from Mississippi, Marion County, tributary to Pearl River, 0.5 mile north of Marion County line, 21 July 1960, RDS 2928, collected by Suttkus and Ramsey; TU 23869,

3 specimens from Mississippi, Copiah County, Copiah Creek, 2.1 miles south of Georgetown, Highway 27, 25 November 1960, RDS 2940, collected by Suttkus and Prudence Menzies; TU 26657, 87 specimens from Mississippi, Marion County, Pearl River, 2.3 miles east of Sandy Hook, 20 October 1961, JSR 61-95, collected by Ramsey and Jamie Thomerson; TU 26695, 1 specimen from Mississippi, Marion County, Holiday Creek, 0.5 mile south of Goss, Highway 13, 21 October 1961, JSR 61-98, collected by Ramsey and Thomerson; TU 26759, 11 specimens from Mississippi, Lawrence County, Fair River, 4.5 miles north of Monticello, Highway 27, 3 November 1961, JSR 61-104, collected by Ramsey and Thomerson; TU 26878, 1 specimen from Mississippi, Marion County, Silver Creek at north limits of Morgantown, Highway 587, 9 December 1961, JSR 61-116, collected by Ramsey and Thomerson; TU 27137, 5 specimens from Mississippi, Lawrence County, Pearl River, 2.5 miles south of Oakvale, 29 August 1962, RDS 3166, collected by R. D. and J. S. Suttkus; TU 27172, 18 specimens from Mississippi, Marion County, 1.5 miles southeast of Morgantown, 30 August 1962, RDS 3168, collected by R. D. and J. S. Suttkus; TU 27299, 12 specimens from Mississippi, Lawrence County, Bahala Creek, 6 miles south of Rockport, Highway 27, 28 October 1961, JSR 61-103, collected by Ramsey and Thomerson; TU 28034, 87 specimens from Mississippi, Marion County, Pearl River, 1.5 miles southeast of Foxworth, 1 December 1962, RDS 3187, collected by R. D. and J. S. Suttkus; TU 28272, 47 specimens from Mississippi, Marion County, Pearl River, 1.5 miles southeast of Foxworth, 17 October 1962, RDS 3172, collected by Suttkus and Clyde D. Barbour; TU 28303, 4 specimens from Mississippi, Marion County, Pearl River, 3 miles southeast of Foxworth, 18 October 1962, RDS 3173, collected by Suttkus and Barbour; TU 28316, 13 specimens from Mississippi, Marion County, Pearl River above mouth of Ten Mile Creek, 6 miles southeast of Foxworth, 18 October 1962, RDS 3174, collected by Suttkus and Barbour; TU 28345, 10 specimens from Mississippi, Marion County, Pearl River, 4 miles north-northeast of Sandy Hook, 0.5 mile upstream from mouth of Hurricane

Creek, 18 October 1962, RDS 3175, collected by Suttkus and Barbour; TU 28373, 7 specimens from Mississippi, Marion County, Pearl River, 2 miles northeast of Sandy Hook, 18 October 1962, RDS 3176, collected by Suttkus and Barbour; TU 28391, 23 specimens from Mississippi, Marion County, Pearl River, 1.5 miles northeast of Sandy Hook, 19 October 1962, RDS 3177, collected by Suttkus and Barbour; TU 28403, 16 specimens from Mississippi, Marion County, Pearl River, 2.3 miles east-southeast of Sandy Hook, 19 October 1962, RDS 3178, collected by Suttkus and Barbour; TU 28429, 24 specimens from Louisiana, Washington Parish, Pearl River, 4 miles east of Angie, 19 October 1962, RDS 3179, collected by Suttkus and Barbour; TU 28534, 240 specimens from Mississippi, Marion County, Pearl River, 1.5 miles southeast of Foxworth, 19-20 December 1962, RDS 3188, collected by Suttkus and William T. Mason; TU 28719, 30 specimens from Mississippi, Marion County, Pearl River, 2.3 miles east of Sandy Hook, 21 October 1961, JSR 61-97, collected by Ramsey and Thomerson; TU 28768, 129 specimens from Mississippi, Marion County, Pearl River, 2.3 miles east of Sandy Hook, 28 December 1962, RDS 3191, collected by Suttkus and Ramsey; TU 28820, 14 specimens from Mississippi, Simpson County, Strong River, 2 miles west of Pinola, Highway 28, 29 December 1962, RDS 3193, collected by Suttkus and Ramsey; TU 29942, 5 specimens from Louisiana, Washington Parish, Pearl River just below sill at Pools Bluff, 4 miles south of Bogalusa, 30-31 August 1963, collected by Suttkus and Gunning; TU 29962, 1 specimen from Louisiana, St. Tammany Parish, Pearl River at River Mile 52, 0.2 mile below mouth of McGehee Creek, 10 September 1963, RDS 3326, collected by Suttkus, Ramsey, and Gunning; TU 29975, 1 specimen from Louisiana, St. Tammany Parish, Pearl River at River Mile 46, 10 September 1963, RDS 3328, collected by Suttkus, Ramsey and Gunning; TU 29989, 1 specimen from Louisiana, St. Tammany Parish, West Pearl River, 5 miles southeast of Talisheek, 11 September 1963, RDS 3332, collected by Suttkus, Ramsey, and Gunning; TU 30010, 17 specimens from Louisiana, Washington Parish, Pearl River just below sill at Pools Bluff, 4 miles south of Bogalusa, 29 September 1963, RDS

3342, collected by Suttkus, Ramsey and Gunning; TU 30025, 2 specimens from Louisiana, St. Tammany Parish, Pearl River, 0.2 mile below mouth of McGehee Creek, 10 October 1963, RDS 3343, collected by Suttkus and Gunning; TU 30040, 2 specimens from Louisiana, Washington Parish, Pearl River just below sill at Pools Bluff, 4 miles south of Bogalusa, 25 October 1963, RDS 3353, collected by Suttkus and Gunning; TU 30149, 32 specimens from Mississippi, Simpson County, Strong River at rapids upstream of Highway 28 bridge, 2 miles west of Pinola, 6 November 1963, RDS 3357, collected by Suttkus and Ramsey.

Noturus phaeus Taylor, 1969, Bull. U. S. Nat. Mus., (282):1-315.

Paratypes: TU 3037, 4 specimens from Mississippi, Lafayette County, tributary to Yocona River, 5.1 miles east of Yocona or 14.7 miles east of Oxford, 23 May 1952, collected by Suttkus, Thomas Cain, Franklin Sogandares-Bernal; TU 3124,⁵ 4 specimens from Mississippi, Lafayette County, tributary to Yocona River, 8 miles east of Oxford, Highway 6, 24 May 1952; TU 14014, 1 specimen from Mississippi, Lafayette County, Yocona River 7.9 miles southeast of Oxford, Highway 334, 12 July 1956, collected by George H. Penn and Joe B. Black; TU 14024, 1 specimen from Mississippi, Alcorn County, 3 miles north of Biggersville, U. S. Highway 45, 12 July 1956, collected by Penn and Black; TU 14036, 2 specimens from Mississippi, Benton County, 0.3 mile west of Michigan City, Mississippi, Highway 7, 11 July 1956, collected by Penn and Black.

Noturus stigmosus Taylor, 1969, Bull. U. S. Nat. Mus., (282):1-315.

Paratypes: TU 19217, 4 specimens from Michigan, Washtenaw County, Huron River at North Territorial Road, 4 miles northwest of Dexter, 31 August 1958, RDS 2750, collected by Suttkus, Carter Gilbert, and William Davis; TU 19246, 6 specimens from Michigan, Washtenaw County, Huron River at North Territorial Road, 4 miles northwest of Dexter, 3 September 1958, RDS 2752, collected by Suttkus, Myrna Andersson, and Thomas Poulson.

Prietella phreatophila Carranza, 1954, Ciencia, Mex., 14(7-8):129-136.

Paratypes: TU 10810, 4 specimens (formerly in the series retained by Carranza at time of publication, subsequently sent to Tulane as a gift; one specimen removed, skeletonized and recataloged as Osteology Collection No. 178) from Mexico, Coahuila, "El Potrero" de Doua Mariana, Municipio de Muzquiz, at the base of Sierra de Santa Rosa, 29 August 1954, collected by Jorge Carranza and C. Bolivar.

Cyprinodontidae

Cualac tessellatus Miller, 1956, Occ. Pap. Mus. Zool. Univ. Mich., 581:1-17.

Paratypes: TU 6557, 32 specimens from Mexico, San Luis Potosi, La Media Luna, about 7 miles south-southwest of settlement of Rio Verde, collected by Richard T. Gregg.

Caproidae

Antigonia combatia Berry and Rathjen, 1959, Quart. Journ. Fla. Acad. Sci. (1958) 21(3):255-258.

Paratypes: TU 18373, 2 specimens from Atlantic Ocean, latitude 07° 31' north, longitude 54° 16' west, off Surinam, 125 fathoms, 8 November 1958, Oregon Sta. No. 2013, collected by M/V Oregon.

Atherinidae

Chirostoma riojai Solorzano and Lopez, 1965, Ciencia, Mex. 24(3-4):145-150.

Paratypes: TU 40173, 2 specimens from Mexico, Mexico, Laguna de Santiago Tilapa, 31 October 1963, LB 1820, collected by A. Solorzano, R. Cruz, R. Aguilar and F. Carmona.

Poblana ferdebueni Solorzano and Lopez, 1965, Ciencia, Mex., 23(5):209-213.

Paratypes: TU 38631, 3 specimens from Mexico, Puebla, Laguna de Almoloya o Chignahuapan, 22 May 1959, L. B. 951, collected by A. Solorzano and T. Obregon.

Serranidae

Pikea mexicanus Schultz, 1958, Proc. U. S. Nat. Mus., 108(3405):321-329.

Paratypes: TU 11004, 6 specimens from Gulf of Mexico, latitude 27° 10' north,

⁵ Given incorrectly in Taylor, 1960: 101 as TU 3134.

longitude $96^{\circ} 20'$ west, 150 fathoms, 5 June 1954, Oregon Sta. 1094, collected by M/V Oregon; TU 11008, 1 specimen from Gulf of Mexico, latitude $27^{\circ} 10'$ north, longitude $96^{\circ} 20'$ west, 150 fathoms, 5 June 1954, Oregon Sta. 1094, collected by M/V Oregon; TU 12972, 11 specimens from Gulf of Mexico, latitude $28^{\circ} 47'$ north, longitude $85^{\circ} 19'$ west, 64 fathoms, 40 foot flat trawl, 7 March 1953, Oregon Sta. 895, collected by M/V Oregon; TU 12985, 1 specimen from Gulf of Mexico, latitude $29^{\circ} 19'$ north, longitude $86^{\circ} 04'$ west, 82 fathoms, 40 foot trawl, 31 October 1953, Oregon Sta. 864, collected by M/V Oregon; TU 14739, 1 specimen from Gulf of Mexico, latitude $27^{\circ} 40'$ north, longitude $95^{\circ} 45'$ west, 100 fathoms, 80 foot balloon trawl, 7 May 1956, Oregon Sta. 1510, collected by M/V Oregon.

Centrarchidae

Ambloplites ariommus Viosca 1936, Copeia, 1936(1):37-45 (currently considered as subspecies, *Ambloplites rupestris ariommus*).

Paratypes: TU 2856, 14 specimens from Louisiana, St. Tammany Parish, Little Bogue Falaya "Falia" Creek, 3 miles north of Covington, 19 May 1935, collected by Percy Viosca and George H. Penn (formerly in the private collection of the late Percy Viosca; given to Tulane about 1955; specimens are green because the original label was a shipping tag with a copper eyelet and the specimens were kept in formalin by Viosca).

Sparidae

Calamus nodosus Randall and Caldwell, 1966, Bull. Los Angeles County Mus. Nat. Hist. Sci., (2):1-47.

Paratype: TU 37765, 1 specimen from Atlantic Ocean off Georgia Coast, latitude $33^{\circ} 42'$ north, longitude $77^{\circ} 11'$ west, 12-20 fathoms, 9 December 1959, Silver Bay Sta. 1507, collected by M/V Silver Bay.

Percidae

Etheostoma collettei Birdsong and Knapp, 1969, Tulane Stud. Zool. and Bot., 15(3): 106-112.

Paratypes: TU 52876, 5 specimens from Louisiana, Union County, Meridian Creek, 1 mile east of Conway, sec. 17, T22N, R1E, 21

May 1956, collected by William R. Taylor and L. W. Lowe.

Etheostoma ditrema Ramsey and Suttkus, 1965, Tulane Stud. Zool., 12(3):65-77.

Holotype: TU 35703, from Georgia, Chattooga County, a spring flowing into a tributary to Mills Creek, tributary to Chattooga River, 4.3 airline miles due west of Lyerly, 18 July 1962, RDS 3134, collected by Suttkus and William T. Mason.

Paratypes: TU 29153, 21 specimens from same collection as holotype; TU 26086, 8 specimens from Georgia, Chattooga County, spring tributary to Mills Creek, tributary to Chattooga River, 5.3 miles west of Lyerly, 19 April 1962, RDS 3052, collected by Suttkus, John S. Ramsey, Jamie Thomerson, and Clyde D. Barbour; TU 27566, 9 specimens from spring tributary to Mills Creek, tributary to Chattooga River, 5.3 miles west of Lyerly, 30 May 1962, JSR 62-57, collected by John S. Ramsey; TU 32981, 43 specimens from Georgia, Chattooga County, spring tributary to Mills Creek, tributary to Chattooga River, 5.3 miles west of Lyerly, 23 June 1964, RDS 3499, collected by Suttkus and Environmental Biology Class.

Etheostoma microlepidum Raney and Zorach, 1967, Am. Midl. Nat., 77(1):93-103.

Paratypes: TU 19479, 19 specimens from Tennessee, Rutherford County, East Fork of Stones River, 6 miles north of Murfreesboro, Highway 231, 7 September 1958, RDS 2758, collected by Suttkus and Myrna Andersson; TU 32983, 71 specimens from Tennessee, Cheatham County, Harpeth River, 8 miles east of White Bluff, Highway 70, 15 July 1964, JSR 64-60, collected by John S. Ramsey and Dan Walton.

Etheostoma moorei Raney and Suttkus, 1964, Copeia, 1964(1):130-139.

Paratypes: TU 22697, 41 specimens from Arkansas, Cleburne County, Devils Fork, Little Red River between Stark and Edgemont, Highway 16, 23 October 1959, RDS 2852, collected by Suttkus, Myrna Andersson, and Bangalore I. Sundararaj; TU 26227, 22 specimens from Arkansas, Van Buren County, Middle Fork, Little Red River at Shirley, 17 August 1962, RDS 3157, collected by Suttkus and William T. Mason; TU 26249, 21 specimens from Arkansas, Van Buren County,

South Fork, Little Red River, 9 miles southwest of Clinton, Highway 95, 17 August 1962, RDS 3158, collected by Suttkus and Mason.

Etheostoma nuchale Howell and Caldwell, 1965, Tulane Stud. Zool., 12(4):101-108.

Paratypes: TU 34591, 20 specimens from Alabama, Jefferson County, Glen Spring at Bessemer, NE $\frac{1}{4}$, Sec. 17, T 19S, R4W, along county Highway 20, 9 September 1964, RDS 3582, collected by Suttkus, John S. Ramsey, and Francis L. Rose.

Poecilichthys whipplii radiusus Hubbs and Black, 1941, Occ. Papers Mus. Zool. Univ. Mich., 429:1-27. (Now known as *Etheostoma radiusum*).

Paratypes: TU 52871, 1 specimen from Arkansas, Garland County, North Fork, Ouachita River, 2.5 miles west of Buckville, 1 June 1939, collected by T. Holder; TU 52872, 5 specimens from Arkansas, Garland County, Cataract Branch, $1\frac{3}{4}$ miles north of Cedar Glade, 2 May 1939, collected by T. Holder; TU 52873, 2 specimens from Arkansas, Garland County, Big Branch, $2\frac{1}{4}$ miles west of Buckville, 16 May 1939, collected by T. Holder. These eight paratypes apparently had been retained at the University of Arkansas by John D. Black subsequent to the description. During 1967, a large part of the University of Arkansas' fish collection was given to Tulane University and thus the transfer of the type material.

Etheostoma rubrum Raney and Suttkus, 1966, Tulane Stud. Zool., 13(3):95-102.

Paratypes: TU 30171, 47 specimens from Mississippi, Copiah County, Bayou Pierre, 8.6 miles southwest of Utica, Highway 18, 7 December 1963, JSR 63-58, collected by John S. Ramsey and Michael D. Dahlberg; TU 31341, 2 specimens from Mississippi, Hinds County, White Oak Creek, tributary to Bayou Pierre, 2.7 miles south of Utica, Highway 18, 1 February 1964, RDS 3378, collected by Edward C. Raney and Suttkus; TU 37305, 4 specimens from Mississippi, Copiah County, Bayou Pierre, 8.6 miles southwest of Utica, Highway 18, 18 March 1965, RDS 3643, collected by Suttkus and Larry Ogren; TU 37451, 53 specimens from Mississippi, Copiah County, Bayou Pierre, 8.6

miles southwest of Utica, Highway 18, 28 April 1965, RDS 3661, collected by Suttkus and Francis L. Rose; TU 40368, 10 specimens from Mississippi, Copiah County, Bayou Pierre, 8.6 miles southwest of Utica, Highway 18, 2 April 1966, RDS 3855, collected by Suttkus and Glenn H. Clemmer.

Percina aurolineata Suttkus and Ramsey, 1967, Tulane Stud. Zool., 13(4):129-145.

Holotype: TU 39573, from Georgia, Gilmer County, Coosawattee River about 200 yards below the mouth of a small spring tributary, 4.2 miles southwest of the center of Ellijay, 18 June 1966, RDS 3910, collected by Suttkus and Environmental Biology Class.

Paratypes: TU 41049, 3 specimens from same collection as holotype; TU 38320, 5 specimens from Georgia, Gilmer County, Cartecay River, tributary to Coosawattee River, 2.9 miles southeast of Ellijay, along Highway 52, 18 June 1965, RDS 3695, collected by Suttkus and Environmental Biology Class; TU 38507, 15 specimens from Georgia, Gilmer County, Coosawattee River, 4.2 miles southwest of Ellijay, 22 June 1965, RDS 3707, collected by Suttkus and Environmental Biology Class; TU 40714, 4 specimens from Georgia, Gilmer County, tributary to Cartecay and Cartecay River, 2.9 miles southeast of Ellijay, along Highway 52, 15 April 1966, RDS 3881, collected by Suttkus and Glenn H. Clemmer; TU 41053, 6 specimens from Georgia, Gilmer County, Cartecay River, 3.1 miles southeast of Ellijay, along Highway 52, 17 June 1966, RDS 3909, collected by Suttkus, Clemmer, and Environmental Biology Class.

Percina lenticula Richards and Knapp, 1964, Copeia, 1964, (4):690-701.

Paratypes: TU 15291, 7 specimens from Alabama, Bibb County, Cahaba River, 2.2 miles north of Centerville, just off Highway 5, 17 May 1957, RDS 2594, collected by Suttkus, Rudolph J. and Helen V. Miller, and John DeAbate.

Clinidae

Starksia y-lineata Gilbert, 1965, Notulae Naturae, No. 379:1-6.

Paratypes: TU 36401, 2 specimens from Caribbean Sea, Grand Cayman Island, "Iron-shore" formation in front of Seaview Lodge,

south side of Georgetown, depth 2–12 feet, collected by Carter R. Gilbert and John C. Tyler.

Microdesmidae

Microdesmus carri Gilbert, 1966, Copeia, 1966, (2):325–332.

Paratypes: TU 36400, 2 specimens from Atlantic Ocean, Costa Rica, Limon Province, east side of Tortuguero lagoon, near mouth, 7 August 1964, collected by D. P. Kelso.

Microdesmus suttkusi Gilbert, 1966, Copeia, 1966, (2):325–332.

Holotype: TU 25110, from Costa Rica, Puntarenas Province, boca de Rio Baru at Dominical, 28 January 1961, RDS 2961, collected by Suttkus, Alfred Smalley, et al.

Paratypes: TU 25130, 1 specimen from Costa Rica, Puntarenas Province, Rio Baru, 1 kilometer north of Dominical, 28 January 1961, RDS 2962, collected by Suttkus, Smalley, et al.; TU 25262, 1 specimen from Costa Rica, Puntarenas Province, at La Barca, 27 February 1960, collected by Salvador Jimenez-C.

Draconettidae

Draconetta oregona Briggs and Berry, 1959, Copeia, 1959, (2):123–133.

Paratypes: TU 18831 (not 188831 as given in description), 3 specimens from Atlantic Ocean, latitude $02^{\circ} 04'$ north, longitude $47^{\circ} 00'$ west, 125 fathoms, 17 November 1957, Oregon Sta. 2080, collected by M/V Oregon.

Gobiidae

Gobiosoma evelynae Böhlke and Robins, 1968, Proc. Acad. Nat. Sci. Philadelphia, 120(3):45–174.

Paratypes: TU 48782, 2 specimens from Atlantic Ocean, Virgin Islands, Anguilla Island, Dowlings Shoal, west of Crocus Bay off north end of Sand Island, 17 July 1965, collected by James C. Tyler and William N. Eschmeyer.

Gobiosoma genie Böhlke and Robins, 1968, Proc. Acad. Nat. Sci. Philadelphia, 120(3):45–174.

Paratypes: TU 48781, 1 specimen from Atlantic Ocean, Bahama Islands, Hog Island, north shore (station 122), 15 March 1953, collected by Charles C. G. Chaplin.

Triglidae

Bellator ribeiroi Miller, 1965, Quart. Jour. Florida Acad. Sci., 28(3):259–266.

Paratypes: TU 37821, 2 specimens from Atlantic Ocean off Colombia, latitude $08^{\circ} 50.5'$ north, longitude $76^{\circ} 53.5'$ west, 37–40 fathoms, 27 May 1964, Oregon Sta. 4899, collected by M/V Oregon.

Peristedion greyae Miller, 1967, Bull. Mar. Sci., 17(1):16–41.

Paratypes: TU 33302, 2 specimens from Atlantic Ocean off North Carolina, latitude $34^{\circ} 15'$ north, longitude $75^{\circ} 54'$ west, 190–200 fathoms, 9 June 1962, Silver Bay Sta. 4159, collected by M/V Silver Bay.

Cottidae

Cottus pygmaeus Williams, 1968, Copeia, 1968, (2):334–342.

Paratypes: TU 34396, 47 specimens from Alabama, Calhoun County, Coldwater Creek, just below Coldwater Springs at town of Coldwater, 31 August 1964, RDS 3571, collected by Suttkus and John S. Ramsey.

Tetraodontidae

Sphoeroides parvus Shipp and Yerger, 1969, Proc. Biol. Soc. Wash., 82:477–488.

Paratypes: TU 9381, 1 specimen from Louisiana, St. Tammany Parish, Lake Pontchartrain, 2 miles west of South Drawbridge of L and N railroad, latitude $30^{\circ} 10'$ north, longitude $89^{\circ} 55'$ west, 5 November 1954, M/V Anna Inez Station 547, collected by Suttkus and party; TU 19038, 2 specimens from Louisiana, Cameron Parish, at jetties along west bank of Calcasieu River at Cameron, 28 April 1957, RFS 7, collected by Rita F. Smith and Michael Guidry; TU 22573, 14 specimens from Louisiana, Jefferson Parish, Gulf of Mexico, 100 yards off Grand Terre Island near Grand Isle, 12 December 1959, collected by Douglas Landwehr and Richard D. Lumsden.

Batrachoididae

Porichthys bathoiketes Gilbert, 1968, Bull. Mar. Sci., 18(3):671–730.

Paratypes: TU 18572, 9 specimens from Atlantic Ocean, latitude $11^{\circ} 27'$ north, longitude $83^{\circ} 11'$ west, 135 fathoms, 9 September

1957, Oregon Sta. 1902, collected by M/V Oregon; TU 18573, 1 specimen from Atlantic Ocean, latitude 16° 07' north, longitude 81° 05' west, 130 fathoms, 24 August 1957, Oregon Sta. 1891, collected by M/V Oregon; TU 18574, 3 specimens from Atlantic Ocean, latitude 16° 38' north, longitude 81° 39' west, 150 fathoms, 22 August 1957, Oregon Sta. 1879, collected by M/V Oregon; TU 19928, 2 specimens from Atlantic Ocean, latitude 16° 39' north, longitude 81° 43' west, 125 fathoms, 22 August 1957, Oregon Sta. 1878, collected by M/V Oregon.

SUMMARY

A brief history of the Tulane University fish collection and a list of type specimens are given. The modern collection was started in 1950 and has grown to nearly two million catalogued specimens in two decades. The following seven holotypes are housed in the Tulane University collection: *Algansea monticola*, *Notropis edwardraueyi*, *Notropis uranoscopus*, *Noturus munitus*, *Etheostoma ditrema*, *Percina aurolineata*, *Microdesmus suttkusi*. There are 30,190 paratypes of 47 different species.

COMPLETE CITATIONS OF ORIGINAL DESCRIPTIONS

- HILDEBRAND, SAMUEL F. 1948. A review of the American menhaden, genus *Brevoortia*, with a description of a new species. *Smithson. Misc. Coll.*, 107(18):1-39.
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TULANE STUDIES IN ZOOLOGY AND BOTANY

Volume 16, Number 4

September 23, 1970

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A SYSTEMATIC REVIEW OF *UROMACER CATESBYI* SCHLEGEL (SERPENTES, COLUBRIDAE)

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ABSTRACT

Uromacer catesbyi occurs throughout Hispaniola and on seven satellite islands. The species is polytypic and the following subspecies are recognized: *U. c. catesbyi* (Tiburon Peninsula, Haiti, west of Momanche), *U. c. cercolineatus* (Isles Petite and Grande Cayemite, Haiti), *U. c. frondicolor* (Ile de la Gonâve, Haiti), *U. c. hariolatus* (Haiti, north of the Cul de Sac Plain), *U. c. inchausteguii* (Isla Saona, República Dominicana), *U. c. insularvacarum* (Ile-à-Vache, Haiti), *U. c. pampineus* (República Dominicana, north of the Valle de Neiba), and *U. c. scandax* (Ile de la Tortue, Haiti). Populations inhabiting the Cul de Sac-Valle de Neiba and the Peninsula de Barahona are assigned intergrade status between *catesbyi*, *hariolatus*, and *pampineus*. The subspecies have differentiated in pattern details and in ventral and subcaudal scale counts. Prototype *catesbyi* presumably divided early into north and south islands populations, the latter with a bold longitudinal line on the lower scale rows. Further differentiation proceeded from these bases; satellite forms are associated with the subspecies on the adjacent mainland.

The colubrid snake genus *Uromacer* Duméril and Bibron is one of four endemic colubrid genera on the Antillean island of Hispaniola. Cochran (1941:329 *et seq.*) recognized six species in the genus: *catesbyi* Schlegel, 1837; *scandax* Dunn, 1920; *frenatus* Günther, 1865; *wetmorei* Cochran, 1931; *dorsalis* Dunn, 1920; and *oxyrhynebus* Duméril and Bibron, 1854. These six species are separable into two groups: one group (*catesbyi*, *scandax*) has the head only slightly elongate with but little modification in the

shape of the preorbital scutellation, whereas the other (the remaining four taxa) has the head very much attenuate, in the fashion of the better known New World mainland genus *Oxybelis*. Of the six forms recognized by Cochran, three (*scandax*, *wetmorei*, *dorsalis*) were considered to be endemic to Hispaniolan satellite islands (Ile de la Tortue, Isla Beata, Ile de la Gonâve, respectively). All *Uromacer* are either green, gray, tan, or some combination of these three basic hues. The long-snouted forms are "vine snakes" in that they are adept climbers and sleep above ground at the tips of branches, whereas the short-snouted forms are apparently somewhat more terrestrial in their activity (but see comments on diet and sites of foraging by Horn, 1969).

Evidence from field studies indicates that there are fewer than six species of *Uromacer*. At the time of Cochran's work, many areas of Hispaniola were unrepresented by collections, and these hiatuses in the distribution of members of the genus may have been responsible for Cochran's interpretation of the distinctness of the various taxa. At most, there appear to be three species (Horn, 1969, recognized four); it is the purpose of this paper to discuss the geographic variation in one of these, *U. catesbyi*, to which species I assign both of the short-snouted taxa: *catesbyi* and *scandax*.

I have examined 265 *U. catesbyi* (including *U. scandax*). Considering the amount of herpetological collecting in Hispaniola in recent years, this is a remarkably small number of snakes. There are other specimens

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in collections, notably in the United States National Museum, which I have not studied, since they in general duplicate material examined in other collections. Nevertheless, *U. catesbyi* seems a less abundant (or possibly less easily secured because of its cryptic coloration) species than other members of the genus.

Collections made in 1963 by myself and party in Haiti easily demonstrated that *U. catesbyi* from the Tiburon Peninsula west of Port-au-Prince differed markedly in life from snakes from north of the Cul de Sac Plain. Additional specimens from both Haiti and the República Dominicana taken between 1964 and 1968 not only confirmed these originally observed differences but also demonstrated the existence of other distinct populations on Hispaniola and its satellite islands. Although there are obvious differences in scutellation between these populations, the most prominent traits are pigmental. Data on the coloration of living individuals are invaluable in a study of the variation in *U. catesbyi*.

Specimens collected by myself and various parties are in the Albert Schwartz Field Series (ASFS). Collections from the República Dominicana were made in 1968 under National Science Foundation Grant GB-7977. I wish to acknowledge the field assistance of Patricia H. Adams, Robert K. Bobilin, Sixto J. Incháustegui, Ronald F. Klinikowski, David C. Leber, John K. Lewis, Dennis R. Paulson, James A. Rodgers, Jr., and Richard Thomas, all of whom aided immeasurably in collecting these snakes in Hispaniola. Mr. Thomas deserves special mention for collecting on Ile Grande Cayemite for me, and Mr. Klinikowski and Drs. Leber and Paulson visited Ile-à-Vache on my behalf. The availability of *U. catesbyi* from Isla Saona is due primarily to the cooperation of Sr. Incháustegui, whose assistance in securing transportation to that little-known island cannot be minimized. In addition to specimens in the ASFS, I have studied snakes in the collections of the Carnegie Museum (CM), the American Museum of Natural History (AMNH), the Museum of Comparative Zoology at Harvard University (MCZ), and the United States National Museum (USNM). These snakes were lent to me by Neil D. Richmond and Clarence J. Mc-

Coy, Jr., Richard G. Zweifel and George W. Foley, Ernest E. Williams, and James A. Peters, respectively, all of whom I wish to thank for their cooperation. A single snake in the collection of Lewis D. Ober (LDO) has also been available to me. Holotypes and paratypes of new subspecies have been designated or deposited in the above collections.

I have counted ventral scales in the manner proposed by Dowling (1951). Paired subcaudal scales also have been tabulated, but, as in many long-tailed snakes, a large number of *U. catesbyi* have incomplete tails. Since the tail is extremely attenuate terminally, even the loss of as little as a centimeter from the end of the tail may profoundly affect the subcaudal count. Accordingly, I have counted the subcaudals of only those snakes that still retain the terminal spine. Supra- and infralabials, loreals, pre- and postoculars, and temporals also were counted. Number of dorsal scale rows behind the head, at mid-body, and before the vent were counted, and each snake was measured (both snout-vent length and tail length) in millimeters.

Uromacer catesbyi (*sensu lato*) is widely distributed on the Hispaniolan mainland and has been taken also on Ile de la Tortue, Ile de la Gonâve, Ile Petite and Ile Grande Cayemite, Ile-à-Vache, and Isla Saona. There are no specimens or records of the species from Isla Beata, where one of the long-snouted forms of *Uromacer* occurs, but almost certainly *U. catesbyi* will be taken on that island. Although there are no specimens from Isla Catalina off the southern Dominican coast, in August 1968 I examined a much decayed *U. catesbyi* that had been killed by members of the Catalina naval garrison a few days previously; thus, the snake does occur on that islet.

Uromacer catesbyi is an inhabitant of wooded situations, but the woods need not be extremely mesic nor high. Presence of shade seems to be a predominant factor, and such lowland situations as lime and cacao groves or scrub and cultivated gardens offer sufficient retreats and shelter for these snakes. Most individuals secured by us were found on the ground or in low bushes. A snake was taken at Centro de Boyá in the República Dominicana, however, as it crawled across the surface of a termitarium at a height of five meters in a tree adjacent

to a road in a patch of broadleaf woods; one of a pair of snakes (which were apparently fighting) was secured from a banana tree at Peneau in Haiti. Perhaps the most interesting site for collection of *U. catesbyi* was a stand of deciduous woods that borders a road near Palo Verde in the República Dominicana. The woods were separated from the road by a barbedwire fence and were surrounded by land planted in sugar cane. Five *U. catesbyi* were taken as they traveled along the barbedwire. When alarmed, the snakes glided away rapidly, using the tops of low shrubs adjacent to the fence as an avenue of escape into the woods beyond. Despite our presence, persistent patrolling of the length of fence continued to reveal more snakes, and it seemed certain that even though alarmed the snakes returned rather quickly to lie upon the shaded barbedwire. Anoles were extremely abundant in the woods and on the fence, and I am confident that the snakes, lying extended on the wire along which the anoles scampered, found this method a simple one of securing food. I have not examined stomach contents of *U. catesbyi* but a *Leiocephalus m. melanochlorus* was regurgitated by a snake taken on Ile-à-Vache. Since this lizard regularly climbs (Schwartz, 1966:48), the fact that it serves as a food item for *U. catesbyi* does not necessarily indicate terrestrial foraging on the part of the snake. Mertens (1939:78) reported a species of *Anolis* and *Hyla dominicensis* as food items for this species. Horn (1969:8-9) listed *Hyla pulcherrilineata*, *H. dominicensis*, *Anolis chlorocyanus*, *A. coelestinus*, *A. cybotes*, and *A. distichus* as food items in *U. catesbyi*. He correctly considered these prey animals as inhabiting trees, tree trunks, and bushes, and stated that *U. catesbyi* "takes arboreal food almost exclusively."

Uromacer catesbyi occurs from below sea level (various localities in the vicinity of Etang Saumâtre and Lago Enriquillo in the Cul de Sac-Valle de Neiba plain) to elevations of 5000 feet (1525 meters) at Peneau on the Montagne Noire in Haiti.

The abundance of *U. catesbyi* varies on the satellite islands. This is remarkably demonstrated by contrasting the situation on Ile-à-Vache with that on Ile de la Tortue. On the former, during two 1-day visits with ample native assistance, we secured 59 *U.*

catesbyi. On Tortue, C. Rhea Warren also spent two days, and, despite promises of remuneration for green snakes, the natives brought no *U. catesbyi* and only a very few *U. oxyrhynchus*. Coupled with the fact that only three Tortue *U. catesbyi* are present in collections, the experience suggests that on Tortue the species is quite uncommon. On Isla Saona, natives brought us both *U. catesbyi* and *U. oxyrhynchus*, more of the latter species being represented. Judged only by my experience, on Ile de la Gonâve *U. dorsalis* outnumbers *U. catesbyi*, but on Ile-à-Vache *U. catesbyi* appears to outnumber *U. frenatus*. Reasons for the abundance or rarity of *U. catesbyi* (or its relative abundance to one of the long-snouted forms) on these satellite islands are unknown.

All populations of *U. catesbyi* are some shade of green both dorsally and ventrally, with the ventral color lighter (more yellow or paler green) than the dorsal color. Those populations associated with the Tiburon Peninsula in Haiti (including snakes from Ile-à-Vache and the Cayemites) have a prominent lateral line in life, usually associated with scale rows one to three, which is pale blue, pale greenish, or white. The dorsal scales usually are very finely edged with black, but in the Isla Saona population, the dark scale edging is very bold and gives a distinctly squamate appearance to the dorsum. Additionally, two populations have dark gray-green markings on the dorsal head scales. All these pattern elements are important in distinguishing the constituent subspecies. In all samples except that from Tortue, there are ample numbers of individuals. There are no color data available for specimens in collections other than the ASFS, and even in my own material I do not have sufficient information to show if differences in dorsal green hue are individual or populational variations. In specimens from other collections, it is often difficult to determine whether the pale lateral line was present, since these snakes become readily discolored after improper preservation, and many long-preserved snakes are now black and without any pattern indications. However, it seems reasonable that, if all freshly collected material from a region shows certain pattern features, these features were also present in older material.

Schlegel's (1837:226-227) description of

Dendrophis catesbyi is brief but sufficiently detailed to allow the name to be positively associated with one population of the species. His data (170 ventrals and 184 subcaudals; uniform grass green above, bluish green below, the two colors separated by a whitish line bordered above by black on the sides of the head) show that the specimen before him almost certainly was a female from the Tiburon Peninsula population. Since collection of the snake was attributed to Alexandre Ricord, a Frenchman who likely collected in Haiti (which at that time was the French colony of St.-Domingue) and who most probably collected in the vicinity of one of the prominent settlements such as Port-au-Prince, where snakes with similar scale counts and pattern occur, the application of nominate status to the Tiburon snakes is affirmed.

SYSTEMATIC ACCOUNTS

Uromacer catesbyi Schlegel

D.(endrophis) catesbyi Schlegel, 1837, Essai sur la physionomie des serpents, 2:226. (Type locality—St.-Domingue).

Uromacer catesbyi Duméril and Bibron, 1854, Erpét. gén., 7:721.

Uromacer scandax Dunn, 1920, Proc. New England Zool. Club, 7:43. (Type locality—"Tortuga Island").

Description: A moderately long (males to 718 mm, females to 908 mm snout-vent length) and slim colubrid snake with 17 or 19 (infrequently 21) scale rows behind the head, 17 scale rows at midbody, and 11 scale rows before the vent; 157 to 177 ventral scales in males, 155 to 179 in females; dorsal scales smooth and without apical pits; head scutellation of the normal unspecialized colubrid type, although the snout is slightly elongate, with modally 1/1 loreals, 1/1 preoculars, 2/2 postoculars, and 1 + 2/1 + 2 temporals; supralabials usually 8/8, infra-labials usually 10/10; anal divided; subcaudals paired, 172 to 208 in males, 159 to 201 in females; dorsum green, the individual scales usually not conspicuously outlined with black along their free margins; lower sides with or without a sharply contrasting longitudinal line, white, pale green, or blue, embracing scale rows 1 to 3 or any combination thereof; venter immaculate pale green, this color paler than the dorsum, often ex-

tending dorsally onto the lower two or three dorsal scale rows and, in the absence of a pale longitudinal lateral line, blending into, or sharply set off from, the darker dorsal green color; a dark green to black mask-like line from the snout through the lower half of the eye onto the temporal region, bounded below by the pale supralabial coloration, and extending onto the neck where it rapidly disintegrates; top of head immaculate green, occasionally (by population) with scattered irregular darker green markings or blotches; hemipenis short (extending about the length of 5 or 6 subcaudals), deeply bifid, the sulcus spermaticus bifurcating to send a branch along each of the distal forks of the hemipenis; the sulcus spermaticus traverses an area which is finely papillose or spinose after first coursing across a prominent median basal lobe or ring which is densely set with minute spines; the non-sulcate surface is laterally covered with closely set enlarged spines which stop abruptly at the papillose region bordering the sulcus, and which more medially are sharply set off from a more or less cordate area, its apex directly basally, of minute spines; this cordate area is expanded distally to form almost a pair of apical discs which form the non-sulcate surface of the distal hemipenial forks. (Description based on the everted organs of ASFS V9565 and ASFS V10304).

Uromacer catesbyi catesbyi Schlegel, 1837

Definition: A subspecies of *U. catesbyi* characterized by the combination of very low number of ventral scales (161 to 169 in males, 156 to 172 in females), high number of subcaudal scales (188 to 202 in males, 173 to 190 in females), a prominent sky-blue lateral longitudinal line usually on scale row 2, but often including 1 and 3, upper surface of head immaculate green, and large size.

Distribution: The Tiburon Peninsula in southwestern Haiti, east to about the level of Momance (Figure 1); specimens from Momance eastward through the Cul de Sac-Valle de Neiba plain and the Peninsula de Barahona in the República Dominicana are interpreted as intermediate between the nominate subspecies and subspecies to the north (see discussion beyond).

Variation: A series of 18 male and 29

female *U. c. catesbyi* from the Tiburon Peninsula west of Momance has the following counts (means and extremes); ventral scales in males 161–169 (164.9), in females 156–172 (163.2); subcaudal scales in males 188–201 (194.6), in females 173–190 (182.1); supralabials usually 8, 8 (45 snakes) with 2 snakes having 7, 8, infralabials usually 10, 10 (40 snakes) with aberrant counts of 8, 8 (1), 9, 10 (3), 9, 11 (1), and 10/11 (1); loreal scales 1, 1 (ASFS X3059 with 0, 0 loreals), preocular scales 1/1 (CM 37788 with 2, 2 preoculars), postocular scales 2/2 (MCZ 70138 with 2, 3 postoculars), temporals 1 + 2, 1 + 2 (CM 37788, MCZ 70135, ASFS X3213 with 1 + 1 bilaterally; MCZ 70138, MCZ 64798 with 1 + 1 unilaterally); largest female (MCZ 65207) with a snout-vent length of 830 mm, largest male (MCZ 70131) 685 mm.

Material from the Port-au-Prince region, where Ricord may have secured the holotype, is intermediate between the nominate subspecies and material from further north; snakes from a short distance west of Port-au-Prince (Momance) clearly resemble those from more distal portions of the peninsula. Even in the Port-au-Prince region, some snakes have the typical pale blue lateral line of *U. c. catesbyi*; this line fades to white in long-preserved snakes and I have little doubt that the holotype possessed this pattern feature while alive. In ventral and subcaudal counts, the holotype agrees with females from both the Tiburon Peninsula (if slight differences in techniques of counting both complements of scales are taken into consideration) and the Port-au-Prince region. It is of course possible that the holotype originated from some more western locality on the peninsula; sites such as Jérémie and Les Cayes have long been prominent seaports for this region. There is little doubt, however, that *U. c. catesbyi* is the proper name for the Tiburon Peninsula snakes.

Specimens from Camp Perrin were dark green (Pl. 22 K 4 to Pl. 24 C 7; all color designations from Maerz and Paul, 1950) in life, with both supra- and infralabials pale green. There was a pale blue (Pl. 25 A 4) longitudinal line of scale row 2, in some specimens including portions of rows 1 and 3, often prominent only anteriorly but in some snakes continuing posteriorly to the vent. The venters (including the chin)

were pale yellow-green (Pl. 17 H 5 to Pl. 17 C 4), this paler coloration extending dorsally onto at least scale row 1, thereby giving a tricolor appearance to the lower sides—dark green, pale blue, and yellow-green, from dorsal to ventral. The iris was gold above and below, and brown anteriorly and posteriorly, thus giving a quadripartite effect; the black mask was outlined above with faintly paler green.

Horn (1969) commented on the occurrence of a gray morph of *U. catesbyi* near Miragoâne. His data were based upon examination of five snakes in the Harvard collection, of which the number of only one (MCZ 66350) was reported. In actuality, there are six *U. catesbyi* in the MCZ collection (25555, 25556, 66349, 66350–51, and 66352) from the Miragoâne region, and another in the Carnegie Museum (CM 37875). I had examined all these specimens prior to the appearance of Horn's paper and considered them in no way different in pigmentation of pattern from other preserved snakes from the Tiburon Peninsula. I have re-examined them in the light of Horn's contention that they were gray above and cream below in life and find that as preserved they are bluish to greenish blue above and pale grayish green below—all colors which occur in preserved *U. catesbyi* from throughout its range. Since green is an especially fugitive color in preservative, and since the precise color of the preserved snake depends upon the original fluid in which it was preserved and the length of time it was stored in the fluid prior to being transferred to the appropriate concentration of alcohol for permanent storage, I do not feel that these snakes (among which must be the four remaining snakes which Horn examined) differed in any strongly chromatic manner from other snakes assigned to *U. c. catesbyi*. The unproved dichromatism in *U. catesbyi* needs further confirmation before it is established.

Scale counts of all subspecies are grouped in Table 1 for ready reference. The various subspecies comparisons are grouped after the subspecies accounts, and this section is in turn followed by a discussion of the probable history of the species on Hispaniola.

Specimens examined: Haiti, Dépt. du Sud, Jérémie, 2 (MCZ 3603); Fond Rouge Daye, nr. Jérémie (not mapped) (MCZ

70128-33); Place Nègre, nr. Jérémie (MCZ 64798-800); Tosia, nr. Jérémie (not mapped) (MCZ 70138); Paroty, nr. Jérémie (not mapped) (MCZ 70137); Mayette, nr. Jérémie (MCZ 70135-36); Lantini, nr. Jérémie (not mapped) (MCZ 70134); Riverdi, nr. Jérémie (not mapped) (MCZ 70127); Trou Bois (MCZ 74521-22); Camp Perrin (ASFS X2976, ASFS X3059-65, ASFS X3153-57, ASFS X3252-53); Petit Trou de Nippes (USNM 80812); nr. Etang Miragoâne (MCZ 25556); *Dépt. de l'Ouest*, Bascap-Rouge, 10 km NE Jacmel (CM 37788-89, MCZ 65207-08); Momance (MCZ 8670); either *Dépt. de l'Ouest*, or *Dépt. du Sud*, Commune Aquin, nr. Miragoâne (CM 37875, MCZ 66349); 6 mi. (12.6 km) from Miragoâne (MCZ 25555); Butète, nr. Miragoâne (MCZ 66350); Mingrette, nr. Miragoâne (MCZ 66352).

Uromacer catesbyi insulaevaccarum,¹
new subspecies

Holotype: CM 45875, an adult female, western end, Ile-à-Vache, *Dépt. du Sud*, Haiti, one of a series collected by native collector on 4 August 1962. Original number ASFS X3539.

Paratypes: ASFS X3381-87, ASFS X3537-38, ASFS X3540-46, same data as holotype; AMNH 103215-24, CM 45877-86, MCZ 92076-85, USNM 165937-48, same locality as holotype, native collectors, 6 August 1962.

Definition: A subspecies of *U. catesbyi* characterized by the combination of low number of ventral scales (162 to 173 in males, 159 to 172 in females), moderate to high number of subcaudal scales (180 to 204 in males, 172 to 200 in females), a pale greenish lateral longitudinal line on scale row 2, occasionally involving a portion of scale row 3, upper surface of head immaculate green, and moderate size.

Distribution: Ile-à-Vache, off the southwestern coast of the Tiburon Peninsula, Haiti (Figure 1).

Description of holotype: An adult female with the following scale counts: ventrals 169, subcaudals 196, supralabials 8/8, infralabials 10/10, loreals 1/1, preoculars 1/2,

postoculars 2/2, temporals 1 + 2/1 + 2; dorsal scale row formula 19-17-11; snout-vent length 712 mm, tail 595 mm.

In life, dorsum green (Pl. 22 L 4), with a pale greenish and faint longitudinal line on scale row 2; venter pale yellow-green with a faint yellow line below the dark green mask-like line; iris golden above, black anteriorly and posteriorly, and dark brown below.

Variation: The series of 25 male and 34 female *U. c. insulaevaccarum* has the following counts (extremes and means): ventral scales in males 162-173 (167.0), in females 159-172 (166.3); subcaudal scales in males 180-204 (192.3), in females 172-200 (184.9); supralabials usually 8/8 (56 snakes) with one snake having 7/8 and two snakes having 9/9, infralabials usually 10/10 (31 snakes) with aberrant counts of 9/10 (2), 10/11 (15), 11/11 (9), and 11/12 (1); loreal scales 1/1 (AMNH 103215 with 0/0; AMNH 103222 with 0/1), preocular scales 1/1 (holotype and USNM 165946 with 1/2), postocular scales 2/2 (AMNH 103220 with 2/3), temporals 1 + 2/1 + 2 (ASFS X3386 with 2 + 2 bilaterally; MCZ 92078, USNM 165946, with 1 + 1 unilaterally); largest female (AMNH 103219) with snout-vent length of 800 mm, largest male (ASFS X3616) 615 mm.

All specimens collected by myself and parties in Ile-à-Vache agree with the definition of the subspecies as far as color and pattern are concerned. One individual had the lateral longitudinal line pale blue like nominate *catesbyi* rather than pale green. The dorsal coloration in the series varied from the dark green of the holotype (Pl. 22 L 4) to a paler hue (Pl. 21 J 5).

Remarks: *U. c. insulaevaccarum* occupies Ile-à-Vache, an island separated from the southern coast of the Tiburon Peninsula of Haiti by a channel 10 kilometers in width. The Ile-à-Vache fauna has several endemic subspecies of reptiles (*Diploglossus costatus nesobous*, *Anolis distichus juliae*, *Anolis coelestinus pecunarius*, *Ameiva taeniura aequorea*, *Dromicus parvifrons rosamondae*), but other reptiles and one amphibian (*Eleutherodactylus pictissimus*, *Diploglossus stenurus*, *Leiocephalus melanochlorus*) whose variation has been studied in detail, do not show any local differentiation. Perhaps the latter group

¹ From *insula* (island) and *vacca* (cow), an allusion to the distribution of the subspecies, Ile-à-Vache.

Table 1. Meristic and pattern data for eight subspecies of *Uromacer catesbyi*.

Subspecies	Number	Ventrals	Subcaudals	Ventrals + subcaudals	Largest (snout- vent length in mm)	Lateral line	Head pattern
<i>catesbyi</i>	18 ♂	164.8 (161-169)	194.6 (188-201)	359.6 (349-370)	685	Pale blue	None
	29 ♀	163.2 (156-172)	182.1 (173-190)	344.5 (336-354)	830		
<i>insulaevaccarum</i>	25 ♂	167.0 (162-173)	192.3 (180-204)	359.5 (341-375)	615	Pale greenish	None
	34 ♀	166.3 (159-172)	184.9 (172-200)	351.4 (339-365)	800		
<i>cereolineatus</i>	6 ♂	166.0 (162-170)	—	—	640	White	None
	3 ♀	165.7 (160-169)	181.0 (177-185)	345.0 (337-353)	410		
<i>haviolatus</i>	16 ♂	171.6 (162-177)	191.6 (183-203)	364.3 (356-375)	645	None	None
	10 ♀	171.4 (167-176)	183.8 (177-194)	353.0 (348-361)	790		
<i>pampineus</i>	13 ♂	167.4 (161-174)	179.8 (172-189)	347.1 (338-358)	610	None	None
	17 ♀	166.8 (163-171)	171.1 (162-183)	338.2 (332-347)	770		
<i>frondicolor</i>	11 ♂	170.4 (167-175)	197.0 (192-208)	376.6 (358-383)	688	None	None
	8 ♀	168.0 (165-171)	177.5 (175-180)	345	755		
<i>scandax</i>	1 ♂	172	—	—	540	None	Present
	2 ♀	175.5 (172-179)	187	360	525		
<i>inchamstegnit</i>	6 ♂	163.3 (160-167)	174.3 (172-176)	338.7 (332-343)	590	None	Present
	17 ♀	163.7 (160-168)	167.6 (159-186)	331.4 (319-350)	795		

represents more recent arrivals than does the former.

In addition to the specimens herein designated paratypes, there is a long series of *U. catesbyi* in the collection of the Museum of Comparative Zoology. Most of our snakes were collected by natives; one was secured in my presence by a boy who took the snake from the crown of a coconut palm with a sloping trunk, which the snake had just ascended with great rapidity.

Uromacer catesbyi cereolineatus,²
new subspecies

Holotype: MCZ 92074, an adult male, vicinity of Pointe Sable, Ile Grande Cayemite, Dépt. du Sud, Haiti, one of a series collected by native collectors on 18 March 1966. Original number ASFS V9563.

Paratypes: ASFS V9561–62, ASFS V9564–66, CM 45887–88, same data as holotype.

Associated specimen: Haiti, Dépt. du Sud, Ile Petite Cayemite, 1 (USNM 80825).

Definition: A subspecies of *U. catesbyi* characterized by the combination of low number of ventral scales (162 to 170 in males, 160 to 169 in females), high number of subcaudal scales (all males with incomplete tails; 177 to 185 in females), a white lateral longitudinal line on scale row 2, and upper surface of head immaculate green.

Distribution: Ile Grande Cayemite (and presumably Ile Petite Cayemite), off the northern shore of the Tiburon Peninsula, Dépt. du Sud, Haiti (Fig. 1).

Description of holotype: An adult male with the following scale counts: ventrals 168, subcaudals 173+ (tail incomplete), supralabials 8/8, infralabials 10/10, loreals 0/0, preoculars 1/1, postoculars 2/2, temporals 1 + 2/1 + 2; dorsal scale row formula 17–17–11; snout-vent length 640 mm, tail 558 mm, incomplete.

In life, dorsum dark green (Pl. 24 H 4), with a prominent white lateral longitudinal line on scale row 2; venter yellow-green; chin and throat very pale green, nearly white; mask-like line bordered above with pale yellow-green. Iris color not noted.

Variation: The series of six male (including one male from Petite Cayemite) and

three female *U. c. cereolineatus* has the following counts (extremes and means): ventral scales in males 162–170 (166.0), in females 160–169 (165.7); total subcaudal scales unknown in males (in three males with nearly complete tails subcaudal counts vary between 173 and 194), in females 177–185 (181.0); supralabials always 8/8, infralabials usually 10/10 (6 snakes) with aberrant counts of 10/11 in two snakes; loreals 1/1 (holotype with 0/0), preocular scales 1/1, postocular scales 2/2 (ASFS V9565 with 1/2), temporals 1 + 2/1 + 2; only female which can be reliably measured (CM 45888) has a snout-vent length of 410 mm, largest male (holotype) 640 mm.

Color in life (Grande Cayemite specimens only; data taken by Richard Thomas) varied from dark to light green (Pl. 24 H 4, Pl. 23 H 2, Pl. 22 I 4), and the lateral longitudinal lines were white in both sexes. In two specimens the white lateral lines faded out on the posterior third of the body, but in other individuals the lines persist to the vent. The venters in the series were pale green to yellow-green, and the chin and throat were very pale green (almost white).

Uromacer catesbyi hariolatus,³
new subspecies

Holotype: USNM 165936, an adult male, 2 mi. (3.2 km) W Trou du Nord, Dépt. du Nord, Haiti, taken by Richard Thomas on 8 April 1966. Original number ASFS V10214.

Paratypes (all from Dépt. du Nord, Haiti): ASFS V10168, 1 mi. (1.6 km) E Terrier Rouge, native collector, 8 April 1966; ASFS V10303, Port Margot, native collector, 10 April 1966; ASFS V10304, 5 mi. (8.0 km) E Limbé, E. Cyphale, 10 April 1966; ASFS V10305, Cap-Haïtien, native collector, 10 April 1966; MCZ 37604, MCZ 37606, Cap-Haïtien, 31 March 1934, Utowana expedition.

Associated specimens: Haiti, Dépt. du Nord Ouest, Môle St. Nicholas (MCZ 64797, MCZ 62697); Bombardopolis (MCZ 62694–96); Dépt. de l'Artibonite, St. Marc (AMNH 49767); Hinche (MCZ 25553–54); Dépt. de l'Ouest, Mirebalais (MCZ

² From *cereus* (waxen) and *linea* (a thread), an allusion to the white lateral longitudinal line.

³ From *harolior* (to predict), an allusion to the expected occurrence of a north island subspecies.

68534); Duvier, nr. Mirebalais (not mapped) (MCZ 68538); Lancironelle, nr. Mirebalais (not mapped) (MCZ 68536-37); Ledie, nr. Mirebalais (not mapped) (MCZ 68543); Fer-à-cheval, nr. Mirebalais (MCZ 68535); Boucan, nr. Mirebalais (not mapped) (MCZ 68539-42); 2.1 mi. (1.9 km) NE Barrage de Peligre (ASFS X2214).

Definition: A subspecies of *U. catesbyi* characterized by a combination of high to very high number of ventral scales (162 to 177 in males, 167 to 176 in females), moderate to high number of subcaudal scales (183 to 203 in males, 177 to 194 in females), no pale lateral longitudinal line but lower sides grading gradually (on the first three scale rows) from yellowish green venter to dark green dorsum, upper surface of head immaculate green, and moderate size.

Distribution: Haiti, north of the Cul de Sac Plain; intergradient specimens (*catesbyi* × *bariolatus*) from the vicinity of Port-au-Prince and the extreme western Cul de Sac (Figure 1).

Description of holotype: An adult male with the following scale counts: ventrals 177, subcaudals 183, supralabials 8/8, infralabials 10/10, loreals 1/1, preoculars 1/1, postoculars 2/2, temporals 1 + 2/1 + 2; dorsal scale row formula 17-17-11; snout-vent length 610 mm, tail 475 mm.

In life, dorsum dark green, venter yellowish green, the ventral color grading gradually on the lowermost three scale rows into the dorsal color, without the interposition of a pale longitudinal lateral line; chin, throat, and supralabials pale yellowish green; mask-like line bordered above by pale yellowish green. Iris color not noted.

Variation: The series of 16 male and 10 female *U. c. bariolatus* has the following counts (extremes and means): ventral scales in males 162-177 (171.6), in females 167-176 (171.4); subcaudal scales in males 183-203 (191.6), in females 177-194 (183.8); supralabials usually 8/8 (23 snakes) with variation of 7/7 (1), and 7/8 (1), and 8/9 (1); infralabials usually 10/10 (24 snakes) with aberrant counts of 9/10 (1) and 10/11 (1); loreal and preocular scales 1/1 in all specimens, postocular scales 2/2 (ASFS X2214 with 2/4, ASFS V10305 with 2/3), temporals 1 + 2/1 + 2 (MCZ 62697 and ASFS V10168 with 1 + 1 unilaterally; MCZ 68538 with 1 + 1 bilaterally); largest female

(MCZ 68539) with snout-vent length of 790 mm, largest male (MCZ 68538) 645 mm.

All specimens were presumably some shade of green in life. The snake from Terrier Rouge was recorded as having the dorsum Pl. 29 A 10 and the venter Pl. 17 C 8 in life, whereas the Port Margot snake had the dorsum about Pl. 21 I 10. The lateral scale rows (1-3) were paler than the balance of the dorsum, and showed a gradation between the ventral color and that of the back. One snake (MCZ 64797) from Môle St. Nicholas on Haiti's Presqu'île du Nord-Ouest, is unique among the *bariolatus* series in that the lower sides are sharply demarcated from the dorsum (but there is of course no longitudinal lateral line). This style of sharply contrasting lower sides agrees better with Dominican *U. catesbyi* (see discussion following) rather than with other *bariolatus*. Three other specimens from the Presqu'île du Nord-Ouest (Môle St. Nicholas and Bombardopolis) are typical *bariolatus* in this feature, however.

Uromacer catesbyi **pampinens**,¹
new subspecies

Holotype: MCZ 92075, an adult female, 2.1 mi (3.4 km) N Hato Mayor, El Seibo Province, República Dominicana, taken by Ronald F. Klinikowski on 18 June 1963. Original number ASFS X7875.

Paratypes (all from the República Dominicana): ASFS V637, 3 km NE Centro de Boyá, San Cristóbal Province, R. Thomas, 22 August 1963; ASFS V1118-19, 2.5 km NW Boca de Yuma, La Altagracia Province, native collector, 4 September 1963; MCZ 16323-24, La Romana, La Romana Province, E. Lieder, 1922; ASFS V2469-70, 5.1 km E. Santo Domingo, Distrito Nacional, D. C. Leber, R. Thomas, 19 June 1964; MCZ 79297-60, Central Ozama, Distrito Nacional, J. D. Lazell, Jr., 29 December 1963; MCZ 57987, Santo Domingo zoo, Distrito Nacional, J. A. Rivero, 29 March 1953.

Associated specimens: República Dominicana, Monte Cristi Province, 2 km NE Palo Verde, 5 (ASFS V1320-24); 1 km S Palo Verde, 1 (ASFS V1351); Laguna de Salodillo, 7 km SE Pepillo Salcedo, 2 (ASFS

¹ From *pampinens* (pertaining to vine tendrils or leaves), an allusion to the green coloration.

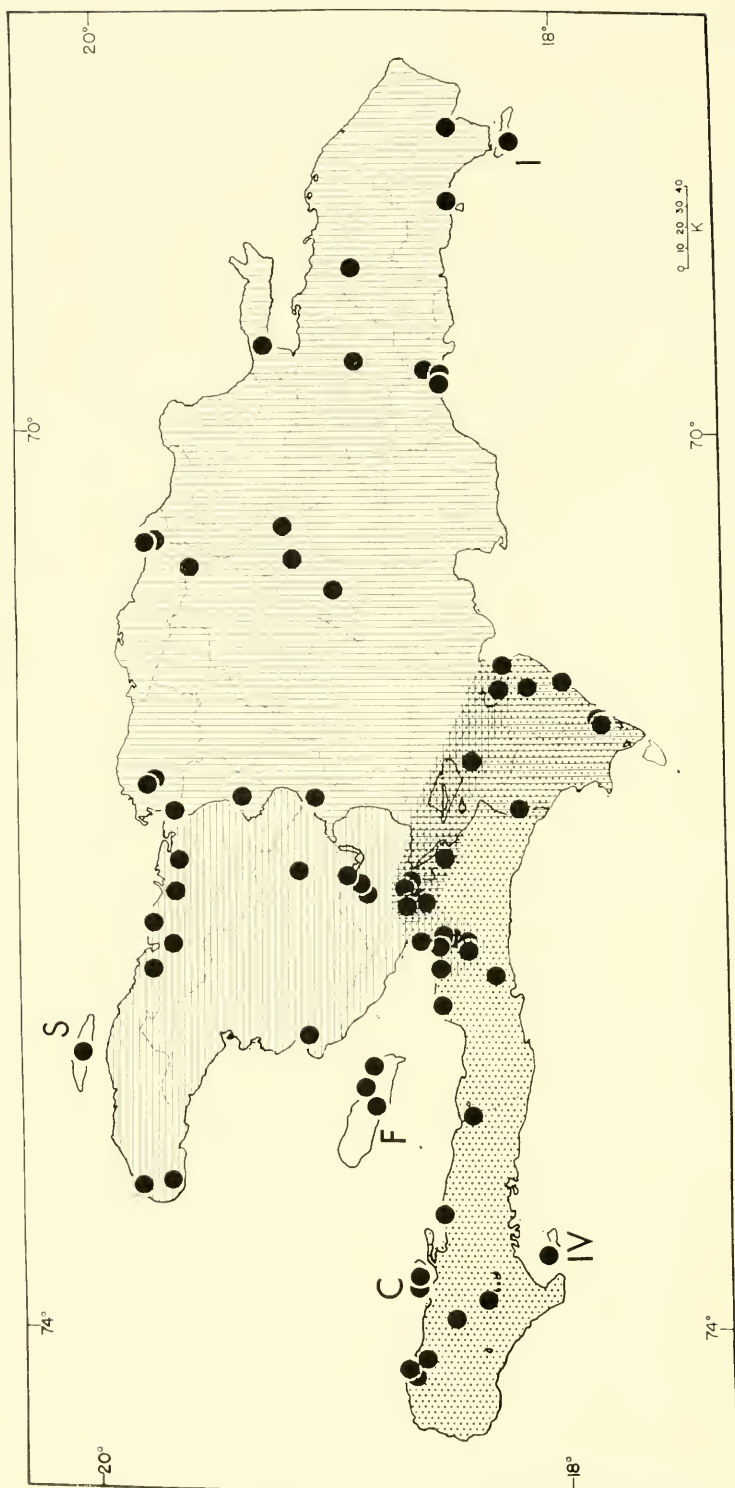


Figure 1. Map of Hispaniola, showing localities whence specimens of *Uromiocrates catesbyi* have been examined and the ranges of the subspecies, as follows: *catesbyi*, horizontal lines; *pampinicus*, vertical lines; *insulariaccarum*, IV; *cereolincatus*, C; *froiducolor*, F; *scandax*, S; *inchausteguii*, I. Area of intergradation between *catesbyi*, *hartiolatus*, and *pampinicus* in the Cul de Sac-Valle de Neiba plain and on the Peninsula de Barahona indicated by overlap of symbols for these three subspecies. The boundary between *hartiolatus* and *pampinicus* along the Dominican-Haitian border is tentative. Large areas, from which no material is available, have been shaded presumptively.

V1458, ASFS V1423); *Dajabón Province*, 1 km S Loma de Cabrera, 900 feet (275 meters), 1 (ASFS V1173); *Puerto Plata Province*, Sosúa, 1 (MCZ 43662); Chocó, 1 (MCZ 13676); 8 km N Pena, 1 (MCZ 57763); *Samaná Province*, Sánchez, 1 (CM 8099); *La Vega Province*, 1 mi. (1.6 km) WSW Constanza, 4000 feet (1220 meters), 1 (ASFS X8731); 12 km NE Jarabacoa, 2000 feet (610 meters), 2 (ASFS V1949, ASFS V14152); 14.4 km E La Vega, 1 (ASFS V4214); *La Estrelleta Province*, Cerro de San Francisco, 3 km E Bánica, 1 (MCZ 57767).

Definition: A subspecies of *U. catesbyi* characterized by the combination of moderate to high number of ventral scales (161 to 174 in males, 163 to 171 in females), low number of subcaudal scales (172 to 189 in males, 162 to 183 in females), no pale lateral longitudinal line but lower sides blue-green to yellow-green on lowermost three scale rows, changing abruptly to green of dorsum, upper surfaces of head immaculate green, and small size.

Distribution: The República Dominicana north of the Valle de Neiba (Figure 1).

Description of holotype: An adult female with the following scale counts: ventrals 164, subcaudals 168 (tail slightly incomplete), supralabials 8/8, infralabials 10/10, loreals 1/1, preoculars 1/1, postoculars 2/2, temporals 1 + 1/1 + 2; dorsal scale row formula 17-17-11; snout-vent length 722 mm, tail 529 mm.

In life, dorsum green (Pl. 29 F 11); first two scale rows, plus half of third scale row, pale blue-green (Pl. 25 B 7); venter and supralabials pale green (Pl. 17 H 8); mask-like line dark green, bordered above by faintly paler green. Iris golden brown above, brown below.

Variation: The series of 13 male and 17 female *U. c. pampineus* has the following counts (extremes and means): ventral scales in males 161-174 (167.4), in females 163-171 (166.8); subcaudal scales in males 172-189 (179.8), in females 162-183 (171.1); supralabials usually 8/8 (29 snakes) with one snake having 7/8, infralabials usually 10/10 (25 snakes) with aberrant counts of 9/9 (1), and 10/11 (3); loreal scales 1/1 (MCZ 79260 with 0/1), preocular scales 1/1 (ASFS V1118 with 2/1, ASFS V4214 with 2/2), postocular scales 2/2 (ASFS

V1173 with 1/2), temporals 1 + 2 1 + 2 (holotype and ASFS V1458 with 1 + 1 unilaterally, MCZ 79257 with 1 + 1 bilaterally, ASFS V637 with 1 + 3 unilaterally); largest female (CM 8099) with snout-vent length of 770 mm, largest male (ASFS V1321) 610 mm.

All specimens were green in life; a female from near Jarabacoa was recorded as being Pl. 19 D 9 above. The venters were uniformly a paler yellow-green (recorded as Pl. 25 A 7 in the Jarabacoa snake); the paler coloration extended onto the lowermost two or three dorsal scale rows as a distinct longitudinal pale area. In some individuals, such as the holotype, the lower sides were pale blue-green, in contrast to both the yellowish venter and the more pure green dorsum. In preserved specimens the lower sides are sharply bicolor in many well-preserved snakes; in other individuals longer preserved or discolored, the bicolor condition of the sides is no longer discernible.

Remarks: No certain intergrades between *bariolatus* and *pampineus* are known from along Dominico-Haitian border. Specimens from localities near this border (Monte Cristi, Dajabón, and La Estrelleta provinces) include snakes which have low subcaudal counts. A male from Monte Cristi (ASFS V1320) has a subcaudal count of 189, the upper extreme of male *pampineus*; the total underbody scales (ventrals subcaudals) of this snake are 357, at the point of overlap of this count between *pampineus* and *bariolatus*. Perhaps the Pepillo Salcedo region is one of extreme intergradation between *pampineus* and *bariolatus*, with the population more closely resembling the Dominican snakes than the Haitian. The snake with the highest female subcaudal count is from La Estrelleta Province; this snake has 183 subcaudals and a total underbody count of 347, the upper extreme of *pampineus* females. It too probably shows the genetic influence of *bariolatus* upon a predominantly *pampineus* population, although with but a single specimen details are lacking.

U. c. pampineus is widespread throughout the República Dominicana and occurs from sea level to elevations of at least 4000 feet (1220 meters) in the Valle de Constanza in the Cordillera Central. The holotype was collected in a *Theobroma* grove, and one snake from near Jarabacoa was collected as

it climbed about the lower branches of a deciduous tree in what is essentially upland (610 meters) pine woods. The specimen from Centro de Boyá was taken as it crawled across a termitarium 4.5 meters above the ground, and the long series from Palo Verde was collected on a barbedwire fence adjacent to anole-rich lowland woods.

Uromacer catesbyi frondicolor,⁵
new subspecies

Holotype: MCZ 93162, an adult male, Degoute, Ile de la Gonâve, Haiti, one of a series collected by George Whiteman in December 1965.

Paratypes (all from Ile de la Gonâve): MCZ 93163–65, same data as holotype; ASFS X2431–32, Etroits, E. Cyphale, 17 July 1962; ASFS X3322, Etroits, E. Cyphale, 26 July 1962; USNM 75926, Anse à Galets, J. S. C. Boswell, 21 September 1928; MCZ 93171, Platon Yeyé (not mapped), G. Whiteman, December 1965; MCZ 93138, Boisederet (not mapped), G. Whiteman, December 1965; MCZ 93167–70, Ravine Fogue (not mapped), G. Whiteman, December 1965; MCZ 93172–73, Bois Boule (not mapped), G. Whiteman, December 1965; MCZ 80830–31, Ti Palmiste, 6 km from Pointe-à-Raquettes, G. Whiteman, summer 1964; USNM 63115, "Gonave Island," W. L. Abbott, 16 March 1920; MCZ 12869, "La Gonâve," G. M. Allen, 1918.

Definition: A subspecies of *U. catesbyi* characterized by a combination of moderate to high number of ventral scales (167 to 175 in males, 165 to 171 in females), (moderate ? to) very high number of subcaudal scales (192 to 208 in males, 175 and 180 in two females), no pale lateral longitudinal line, the lower sides grading gradually (on the first three scale rows) from the light green venter to the dark green dorsum, upper surfaces of head immaculate green, and moderate size.

Distribution: Ile de la Gonâve, Haiti.

Description of holotype: An adult male with the following scale counts: ventrals 171, subcaudals 193, supralabials 8/8, infralabials 10/10, loreals 1/1, preoculars 1/1, postoculars 2/2, temporals 1 + 1/1 + 3; dor-

sal scale row formula 18–17–11; snout-vent length 688, tail length indeterminate because of damaged tail.

Preserved, the holotype is blue-green above, slightly paler below. The supralabials are concolor with the venter, and the black mask-like line is prominent and bordered above on the temporal region by pale bluish green. Iris color indeterminable.

Variation: The series of 11 male and 8 female *U. c. frondicolor* has the following counts (extremes and means): ventral scales in males 167–175 (170.4), in females 165–171 (168.0); subcaudal scales in males 192–208 (197.0), in two females with complete tails 175–180 (177.5); supralabials 8/8 in all specimens, infralabials usually 10/10 (11 snakes) with aberrant counts of 9/10 (3), 10/11 (3), 11/11 (2) and 11/12 (1); loreal scales 1/1, preocular scales usually 1/1 (MCZ 93168 and MCZ 93165 with 1/2), postoculars 2/2 (MCZ 93138 with 1/2), temporals 1 + 2/1 + 2 (ASFS X3432, MCZ 12869, MCZ 93138 with 1 + 1 unilaterally; MCZ 93170 with 1 + 1 bilaterally; holotype with 1 + 1/1 + 3); largest female (MCZ 80830) with snout-vent length of 755 mm, largest male (holotype) 688 mm.

The color of the three *U. c. frondicolor* seen in life was recorded as light green below and dark green above, and there was no blue lateral line. The remaining paratypes have been preserved for various periods, and little can be said about the coloration and pattern in life of this subspecies.

Remarks: The relatively few specimens of *U. c. frondicolor* available suggest that the species is uncommon on Ile de la Gonâve. One of the specimens from Etroits was taken by natives in a lime grove. Since so few of the localities for *U. c. frondicolor* are precisely locatable, the altitudinal distribution of the subspecies is unknown; however, Etroits is on the coast in an extremely xeric situation and Ti Palmiste lies inland at an elevation of about 400 meters.

Uromacer catesbyi scandax Dunn, 1920

Definition: A subspecies of *U. catesbyi* characterized by a combination of high to very high number of ventral scales (172 in single male, 172 to 179 in two females), high (?) number of subcaudal scales (187 in female with complete tail), no pale lateral

⁵ From *frons* (leaf) and *color* (color), an allusion to the green color.

longitudinal line and, apparently, lower sides not set off chromatically from the upper dorsum, and upper surface of head with scattered darker areas (in life green?) on a paler ground at least in juveniles.

Distribution: Ile de la Tortue, off the northern Haitian coast (Figure 1).

Variation: A single male *U. c. scandax* has 172 ventrals, subcaudals indeterminate, 8/8 supralabials, 10/10 infralabials, 1/1 loreals, 1/1 preoculars, 2/2 postoculars, 1 + 2/1 + 2 temporals, dorsal scale row formula 19-17-11, snout-vent length 540 mm; two females have 172 and 179 ventrals (mean 175.5), 187 subcaudals in one specimen, 8/8 supralabials, 10/10 infralabials, 1/1 loreals, 1/1 preoculars, 2/2 postoculars, 1 + 2/1 + 2 temporals, 19-17-11 and 17-17-11 dorsal scale rows; one female has a snout-vent length of 525 mm and a tail length of 410 mm.

The status of the Tortue population of *U. catesbyi* remains equivocal. Dunn (1920) described *U. scandax* from a single female from "Tortuga Island," and Cochran (1941: 334) accepted this form as a species distinct from *U. catesbyi*. Cochran also (*op. cit.*: 332-333) considered two other specimens from Tortue as *U. catesbyi*, thereby implying that two short-snouted species of *Uromacer* occurred on that island. Mertens (1939:78), however, considered *scandax* only subspecifically related to *U. catesbyi*. I have studied the three specimens available to Cochran and can see no reason either to consider *scandax* a species distinct from *catesbyi* or to exclude the two other Tortue specimens from *scandax*. These three specimens, considered together, seem to indicate that *scandax* is a moderately well defined subspecies of *U. catesbyi*. Lack of an adequate series makes meristic comparisons of *scandax* with other *U. catesbyi* subspecies difficult. However, the ventral counts of two female *scandax* (172 and 179) are at the upper limit of ventral counts for the species (155 to 179), and the count for the single male (172) is high in the total range of this count in male *U. catesbyi* (157-177). Except for the high ventral counts in female *scandax*, the next highest counts occur in female *U. c. hario-latus*, which occurs on the adjacent mainland of Haiti.

The two smaller specimens of *U. c. scandax*

(USNM 59920, MCZ 37607) are peculiar in that they are now a dull grayish green dorsally and are heavily stippled with dark gray-green ventrally—a chromatic development not matched by any other specimens of *U. catesbyi*. The adult holotype (USNM 59438) presently is colored like comparably aged specimens. It is likely that fresh specimens of *scandax* will demonstrate chromatic differences, at least in immature specimens, between the Tortue subspecies and those elsewhere.

Specimens examined: Haiti, Ile de la Tortue (USNM 59438—holotype, USNM 59920, MCZ 37607).

Uromacer catesbyi inchausteguii,⁶
new subspecies

Holotype: CM 45876, an adult female, environs of Mano Juan, Isla Saona, República Dominicana, one of a series collected by native collectors on 28 December 1968. Original number ASFS V16157.

Paratypes (all from Isla Saona): ASFS V16158-59, ASFS V16177, same data as holotype; ASFS V3068, same locality as holotype, R. Thomas, 19 July 1964; MCZ 92086-90, same locality as holotype, native collectors, 13 August 1968; AMNH 103225-29, USNM 165950-54, same locality as holotype, native collectors, 14 August 1968; USNM 165949, same locality as holotype, native collector, 29 December 1968; LDO 7-5535, same locality as holotype, native collector, 30 December 1968; ASFS V16321, 2.5 mi. (4.0 km) NW Mano Juan, J. A. Rodgers, Jr., 29 December 1968.

Definition: A subspecies of *U. catesbyi* characterized by the combination of low to very low number of ventral scales (160 to 167 in males, 160 to 168 in females), very low number of subcaudal scales (172 to 176 in males, 159 to 186 in females), no pale lateral longitudinal line, but lower sides (scale rows 1-3) a distinctly paler green than the dorsum, all dorsal scales with a distinct black edging to give a definitely squamate appearance, upper side of head with dark green markings on a paler green ground, and small size.

Distribution: Isla Saona, off the south-

⁶ In honor of Sixto J. Inchaustegui who was responsible for the opportunity to collect most of the specimens of this subspecies.

eastern tip of the República Dominicana (Figure 1).

Description of holotype: An adult female with the following scale counts: ventrals 161, subcaudals 163, supralabials 8/8, infralabials 10/10, loreals 1/1, preoculars 1/1, postoculars 2/3, temporals 1+2/1+2, dorsal scale row formula 19-17-11; snout-vent length 680 mm, tail 484 mm.

In life, dorsum green, the lowermost three scale rows distinctly paler green than dorsum, a lateral extension of the ventral pale green color; throat and supralabials whitish (very pale green), black mask-like line margined above by very pale green; internasals, prefrontals, supraoculars, and parietals with dark grayish green flecks, dashes, or rectangular figures (on prefrontals), all very conspicuous in life. Iris color unrecorded.

Variation: The series of 6 males and 17 females has the following counts (extremes and means): ventral scales in males 160-167 (163.3), in females 160-168 (163.7); subcaudal scales in males 172-176 (174.3), in females 159-186 (167.6); supralabials 8/8, infralabials 10/10, with two snakes having 9/10; loreal scales 1/1 (ASFS V14895 with 0/0), preocular scales 1/1, postocular scales 2/2 (holotype and ASFS V14894 with 2/3), temporals 1+2, 1+2; largest female (ASFS V3068) with snout-vent length of 795 mm, largest male (AMNH 103225) 590 mm.

The entire series of *U. c. inchausteguii* agrees with the description of the holotype in having the dorsal scales edged with black, these giving a distinctly squamate appearance to the back, and in having flecks, dashes, or small irregular dark figures on the dorsal head scales. The lower sides (scale rows 1-3) are in life often a paler shade of green, contrasting distinctly with the darker green back, but this feature sometimes is lost after preservation.

Remarks: *U. c. inchausteguii* appears to be fairly common in the environs of the village of Mano Juan. The specimen taken by Rodgers was secured in open broadleaf forest as it crawled on leaf litter. Of the two species of *Uromacer* on Isla Saona, *U. catesbyi* appears to be outnumbered by *U. oxyrhynchus*, since more specimens of the latter species were brought to us by native collectors.

COMPARISONS

Uromacer catesbyi has been shown to be divided into eight subspecies. Three of these subspecies are obviously interrelated more closely than they are to the balance of the subspecies. The subspecies *catesbyi*, *insulaevaccarum*, and *cereolineatus* possess a pale lateral line on scale rows 1 to 3, whereas the remaining five subspecies lack this pattern feature. The three lineate taxa differ from each other in the color of the lateral line (pale blue in *catesbyi*, pale greenish in *insulaevaccarum*, and white in *cereolineatus*). In addition to the differences in lateral line pigmentation, both sexes of *U. c. catesbyi* have lower mean numbers of ventral scales than do both sexes of *insulaevaccarum* (male *catesbyi* 164.8, male *insulaevaccarum* 167.0; female *catesbyi* 163.2, female *insulaevaccarum* 166.3), although the differences are not striking. In subcaudal scale counts, the situation is anomalous, since male *insulaevaccarum* have a lower mean (192.3) than do male *catesbyi* (194.6), and female *insulaevaccarum* have a much higher mean (192.3) than do female *catesbyi* (182.1). These two subspecies reach approximately the same size.

Comparison of *catesbyi* and *insulaevaccarum* with *cereolineatus* is made difficult by the short series of the latter subspecies, and the fact that no male *cereolineatus* have complete tails. There are also no obviously adult female *cereolineatus*, so that size comparisons are not possible. At least male *cereolineatus* resemble male *insulaevaccarum* in maximum known size, rather than there being a resemblance between *cereolineatus* and adjacent *catesbyi* in this feature. Total underbody scale counts (ventrals + subcaudals) of female *cereolineatus* are close, both in means and extremes, to those of *catesbyi* and are lower than those of *insulaevaccarum*.

The remaining five subspecies (*bariolatus*, *pampineus*, *frondicolor*, *scandax*, *inchausteguii*) differ as a group from the western subspecies *catesbyi-insulaevaccarum-cereolineatus* series in lacking a lateral line. *U. c. bariolatus* is characterized by having a gradual change from the ventral coloration to that of the dorsum and in having a higher mean number of ventral scales in both sexes in comparison with all the western subspecies

(mean in male *bariolatus* 171.6, means in males of western subspecies 164.8–167.0; female *bariolatus* 171.4, means in females of western subspecies 163.2–166.3). *U. c. pampineus* resembles *bariolatus* in being all green and without a lateral line, but *bariolatus* lacks the strongly contrasting lower scale rows which *pampineus* possesses. The subcaudal counts of *bariolatus* are consistently higher (183–203 in males, 177–194 in females) than in *pampineus* (172–189 in males, 162–183 in females); the ventral counts of the two subspecies are comparable, with *pampineus* averaging a few less ventrals than *bariolatus*. If total underbody scale counts are used to distinguish the two populations, almost complete separation of individuals of both sexes is achieved (356 to 375 in male *bariolatus*, 338 to 358 in male *pampineus*; 348 to 361 in female *bariolatus*, 332 to 347 in female *pampineus*).

U. c. frondicolor differs from *pampineus* in lacking contrastingly colored lower sides and in having a higher number of subcaudal scales (at least in males; only two female *frondicolor* have complete tails). Male *pampineus*, with subcaudal counts of 172 to 189, are completely separable from male *frondicolor* with subcaudal counts of 192 to 208. Of all the subspecies of *U. catesbyi*, *frondicolor* has the highest counts of subcaudal scales. *U. c. frondicolor* most closely resembles adjacent *U. c. bariolatus* in dorsal and lateral color and pattern. *U. c. frondicolor* averages less ventral scales in both sexes than does *bariolatus* (male *frondicolor* 170.4, male *bariolatus* 171.6; female *frondicolor* 168.0, female *bariolatus* 171.4), although the extremes in male *frondicolor* are embraced by the extremes in male *bariolatus*. The situation in subcaudals is anomalous, since the male *frondicolor* have a higher mean (197.0) than do male *bariolatus* (191.6); the subcaudal counts of the two female *frondicolor* on the other hand lie below and at the lower extreme of subcaudal counts in female *bariolatus*. It seems likely that additional female *frondicolor* will show that, in this sex also, the subcaudal count has both a higher mean and upper extreme than in female *bariolatus*.

The remaining two subspecies, *scandax* and *inchausteguii*, differ from all others in that both have dark cephalic markings; these markings occur apparently only in juveniles

in *scandax* and in all specimens in *inchausteguii*. Although *scandax* is represented by only three specimens, the ventral counts from these three snakes are at the upper extreme (females) or high (male) for the species. On the other hand, *inchausteguii* has the lowest mean number of subcaudal scales and a low mean number of ventral scales. Total underbody scale counts in *inchausteguii* are 332 to 343 in males, 319 to 350 in females. Male *inchausteguii* are completely separable from male *catesbyi*, *frondicolor* and *bariolatus*, when this count is used as an index, and there is very little overlap between *inchausteguii* and male *insulaevaccarum* and *pampineus*. As far as females are concerned, there is little overlap between total underbody counts of *inchausteguii* and *bariolatus* (348–361). The darkly margined scales of *inchausteguii* differentiate that subspecies from all others.

DISCUSSION

Uromacer catesbyi, as defined here, is comprised of eight subspecies, three of which occur on the main island (*catesbyi*, *bariolatus*, *pampineus*) and five on satellite islands (*insulaevaccarum*, *cereolineatus*, *frondicolor*, *scandax*, *inchausteguii*). The distribution of the subspecies in *U. catesbyi* is similar to that of *Dromicus parvifrons* Cope (see Thomas and Schwartz, 1965); in that colubrid snake, nine subspecies are recognized, four of which occur only on the main island, four on the satellites, and one on both a satellite island and the adjacent mainland. Details of subspecific boundaries in *U. catesbyi* and *D. parvifrons* on Hispaniola are not comparable, although a distinct subspecies of each occurs on the Tiburon Peninsula. I have examined only a few specimens of *U. catesbyi* from the Península de Samaná in the northeastern República Dominicana. This peninsula, with its narrow swampy neck, has been a center of differentiation for several species of amphibians and reptiles (*Eleutherodactylus weinlandi*, *Diploglossus stenurus*, *Dromicus parvifrons*); it is possible that still another subspecies of *U. catesbyi* inhabits the Península de Samaná.

No mention has thus far been made of the complexities of the interrelationships between the subspecies *catesbyi*, *bariolatus*, and *pampineus* in, and south of, the Cul de Sac-

Valle de Neiba plain which separates the old north and south (*sensu* Williams, 1961) islands of Hispaniola, and on the Península de Barahona. A discussion of the problems in this region, and the interpretation of these problems is now presented.

The region of intergradation between nominate *catesbyi* and *bariolatus* is in the vicinity of Port-au-Prince and the western extreme of the Cul de Sac Plain in Haiti. Two specimens from Port-au-Prince (MCZ 60154, MCZ 37599), one from Pétienville (MCZ 60162) in the mountains south of Port-au-Prince, and three from Damien in the Cul de Sac north of Port-au-Prince (MCZ 60158–60) have a longitudinal pale lateral line (presumably blue in life) on the lower-most scales rows (scale row 2 in all, expanding to scale row 1 in one snake and to row 3 in two snakes). Other snakes from this general region (Mont Cabaño, Morne Decayette, Morne l'Hôpital, Delmas, Peneau—a total of 15 additional specimens) at present lack any indication of the lateral line. The snake from Peneau was examined while living and I can verify the absence of the lateral line. Thus, snakes from the area included by Morne Decayette in the west, Damien in the north, Delmas in the east, and Peneau and Mont Cabaño in the south I regard as intermediate in pattern between *catesbyi* and *bariolatus*. Snakes from the southern versant of the Massif de la Selle in this region (Bascap-Rouge) are typical *U. c. catesbyi* and show no *bariolatus* influence.

The Hispaniolan south island is comprised of both the Tiburon Peninsula in Haiti and the Península de Barahona in the República Dominicana. The north island includes the balance of Hispaniola north of the Cul de Sac-Valle de Neiba plain. In a large number of species of amphibians and reptiles, the south island area is occupied by populations subspecifically distinct from those of the north island.

A reasonable assumption would be that *U. c. catesbyi* is the form occurring on the Península de Barahona, but such does not seem to be the case. A series of 12 snakes from various Barahona localities, including the city of Barahona itself and its immediate environs, as well as localities (Oviedo, Peder-nales) well south on the peninsula, is available; none of these snakes has the distinctive

U. c. catesbyi lateral line. Two of the specimens were collected by myself and parties, and neither was recorded as having a pale lateral line; the balance of the Barahona material is from other collections and color and pattern data are not available. Thus I interpret the absence of the lateral line in all specimens from this region as a constant Barahona feature. The means of ventral scales in the Barahona snakes (164.5 in males, 164.4 in females) are quite comparable to similar means (164.8 and 164.4, respectively) in *catesbyi*. There are no Barahona males with complete tails, but the female subcaudal mean (179.0) is similar to that in female *catesbyi* (182.1). The largest female *U. catesbyi* examined (MCZ 57765), with a snout-vent length of 908 mm, is from the Península de Barahona; *U. c. catesbyi* is a large snake, although the largest Tiburon female has a snout-vent length of 830 mm.

The Cul de Sac-Valle de Neiba plain presently connects the previous Hispaniolan north and south islands. If this plain (in places lower than sea level) was at times a strait separating the two islands and was recolonized after its emergence, it seems reasonable that the *U. catesbyi* populations in the plain would show a mixture of characteristics of the subspecies to the north and the south. I have pointed out above that *bariolatus* and *catesbyi* intergrade in the extreme western portion of the Cul de Sac. There is a series of 15 snakes from the balance of the plain (localities from Eaux Gaillées in Haiti to Cabral in the República Dominicana, five of which were collected by Richard Thomas); none of these shows any trace of a lateral pale stripe, nor any tendencies toward the nominate subspecies. Nine males have a ventral mean of 166.5—intermediate between the mean ventral count of *catesbyi* + Barahona males on one hand, and *bariolatus* on the other. Six females from this region have a ventral count mean of 166.8, again intermediate between the same two samples. The subcaudal mean (186.8) of six males, however, is much lower than that of ten *catesbyi* males (194.6), although the extremes overlap very broadly; four females from the Cul de Sac-Valle de Neiba have a subcaudal mean (182.8) almost identical with that of 11 female *catesbyi* (182.1).

Specimens of *U. catesbyi* from Haiti (*bari-*

olatus) differ from those from the República Dominicana (*pampineus*) in number of subcaudal scales, the Dominican snakes with much lower ranges and means. It is possible that *pampineus* (with lower number of subcaudals) has influenced the Cul de Sac-Valle de Neiba snakes to some extent, thereby accounting for the low number of subcaudals in males from the Cul de Sac-Valle de Neiba.

I interpret the Cul de Sac-Valle de Neiba snakes as intermediate between *catesbyi* (whose influence is most clearly shown in the laterally striped pattern at the extreme western end of the Cul de Sac), *bariolatus* (whose influence is most clearly shown in the basic dorsal color and absence of a longitudinal line in the greater portion of the sample), and *pampineus* which has contributed toward the lower number of subcaudal scales.

The Barahona population is peculiar. In color and pattern it agrees with *pampineus* north of the Valle de Neiba, rather than with *catesbyi* to the west; in ventrals, the Barahona snakes are like *catesbyi* rather than *pampineus*, and in subcaudals they are like *bariolatus* (and intergradient specimens from the Cul de Sac-Valle de Neiba). Although there might be justification in the future for considering the Península de Barahona populations as a subspecies distinct from all others, it seems prudent at this time to regard them as extreme intergrades between *catesbyi* and *pampineus*.

The above discussion is based upon the following suite of specimens, grouped according to the areas mentioned:

I. Port-au-Prince and vicinity (*catesbyi* × *bariolatus*): *Haiti, Dépt. de l'Ouest*, Port-au-Prince (MCZ 60149–50, MCZ 60152–57, MCZ 37599); Morne Decayette (MCZ 62698); Source Leclerc, Morne Decayette (MCZ 65969); Delmas (MCZ 65970–71); Damien (MCZ 61058–61); Source Bariajoux, Morne l'Hôpital (not mapped) (MCZ 65972); Pétienville (MCZ 60162); Furcy, Mont Cabaïo (MCZ 45743); Peneau, 5000 feet (1525 meters) (ASFS X1572).

II. Cul de Sac-Valle de Neiba (*catesbyi* × *bariolatus* × *pampineus*): *Haiti, Dépt. de l'Ouest*, 13.1 km E Croix des Bouquets (ASFS V8144, ASFS V8345, ASFS V8307); Eaux Gaillées (MCZ 60168–70); Thomazeau

(MCZ 12864–65); Tête Source, 1.4 mi. (2.2 km) NNE Thomazeau (ASFS V8197); between Thomazeau and Gloré (MCZ 60171); Manneville (MCZ 8747); La Source, E of Fond Parisien (ASFS V8134); *República Dominicana, Independencia Prov.*, Duvergé (AMNH 40993–94); *Barahona Prov.*, woods at Cabral (AMNH 52397).

III. Península de Barahona (*catesbyi* × *pampineus*): *República Dominicana, Barahona Prov.*, Barahona (MCZ 43804–05); Palomino Springs, nr. Barahona (not mapped) (AMNH 59750); Valle de Polo (AMNH 51426–27, AMNH 51422); Hermann's finca, nr. Paraíso (AMNH 51424); 3.5 mi. (5.6 km) from Paraíso (AMNH 51428); *Pedernales Prov.*, 13.1 mi. (21.0 km) SW Enriquillo (ASFS V4425); Oviedo (MCZ 57765–66); 19 km N Pedernales, 1000 feet (305 meters) (ASFS V2697).

Horn (1969) proposed an hypothetical history of the genus *Uromacer* which he considered to be composed of four species. *Uromacer catesbyi* he regarded as the most primitive of the species, since it is the least specialized morphologically (all other species are long-snouted, attenuate snakes) and has a dietary repertory which is composed of arboreal animals. (Presumably arboreality is the original niche for the genus, from which situation the remaining species have become more terrestrial.) Horn further suggested that an ancestral colubrid (perhaps an unspecialized *Alsophis*—type snake) gave rise to both a proto-*catesbyi* and a proto-*frenatus* (the latter one of the long-snouted taxa), which were, respectively, the *Uromacer* of the north and south Hispaniolan islands. Although this is a possibility, the taxonomic status of the long-snouted forms precludes any more definitive statement of the early history of the genus. Whatever the early division of the genus, surely there was a basic division into short- and long-snouted forms, but I remain unconvinced that proto-*catesbyi* is the north island analogue of south island proto-*frenatus*. It seems likely to me that, early in the history of proto-*catesbyi*, this group of snakes invaded the south island from the north island, and that the presence of a lineate lateral pattern in the Tiburon-Vache-Cayemites subspecies represents one old line of evolution from proto-*catesbyi* and the non-lineate subspecies represent the

other. Although it is customary to consider that loss of a character is the more advanced condition (and thus the Tiburon-Vache-Cayemites subspecies would represent the primitive forms since they possess a pale lateral line), the non-lineate subspecies occupy a much greater area and the absence of a lateral line would seem in this case to be the primitive rather than the advanced condition.

Whatever the details, it seems certain that *U. catesbyi* was early split into two stocks, corresponding to the old north and south islands of Hispaniola. One of these (that on the south island) had a pale lateral longitudinal line (*catesbyi*) and from this stock arose *insulaevaccarum* and *cereolineatus*. Both subspecies retain the lineate lateral pattern but have diverged in the color of the lateral line (from blue to pale green or white). The north island stock, separated from its relatives on the south island by the then submerged Cul de Sac-Valle de Neiba plain, lacked a lateral longitudinal pale line but maintained a more or less uniform dorsal color (although the lower sides may be lighter in contrast to the more dorsal coloration).

With the elevation of the interisland strait, the south island *catesbyi* and the north island *bariolatus* and *pampineus* once more came into contact and intergraded with one another. Intergradation is evident in the western Cul de Sac, where some snakes retain the blue lateral line of *catesbyi* and some do not. In the rest of the Cul de Sac-Valle de Neiba plain, the snakes present a mixture of scutellar characteristics derived from *catesbyi*, *bariolatus*, and *pampineus*. The most unusual situation is that on the Peninsula de Barahona, where the snakes seem to represent intergrades between *catesbyi* and *pampineus*; typical blue-lined *catesbyi* occur no closer to the República Dominicana in the region of the Peninsula de Barahona than Bascap-Rouge on the southern slope of the Massif de la Selle in Haiti. Although the Barahona situation is not clear, it is possible that northern *pampineus* and southern *catesbyi* were long in contact in the Barahona region (this contact possibly of longer duration than the final, complete closure of the interisland strait) with consequently greater opportunity for genetic mixing. There remains

the possibility that, as in the case of the subspecies of *Dromicus parvifrons* (Thomas and Schwartz, 1965:69-70), the Peninsula de Barahona populations of *U. catesbyi* show influence from an as yet undiscovered Isla Beata population, if it in fact exists.

The two north island subspecies *bariolatus* and *pampineus* present a puzzle. I cannot arrive at any reason for the two subspecies to meet at approximately the Dominico-Haitian border as they appear to do. Along this border there is a more or less continuous montane barrier (Montagnes du Trou d'Eau-Sierra de Neiba; Massif du Nord-Cordillera Central); these ranges lie at right angles to the international boundary and intermontane valleys should afford easy access between the two subspecies. Additionally, *U. catesbyi* occurs at high elevations, and mountains should not be effective barriers to these snakes.

Two of the satellite subspecies, *scandax* and *inchausteguii*, differ from all other populations in having a patterned head (apparently only in juvenile *scandax*). The islands inhabited by these subspecies, Tortue and Saona, lie diametrically opposed to Hispaniola proper, one at the northwest (Tortue), the other at the southeast (Saona). That such a pigmental trait occurs in two widely separated populations of *U. catesbyi* is perplexing. A comparable situation is the basically black ground color of all the satellite populations of *Dromicus parvifrons*, in contrast to most of the mainland snakes.

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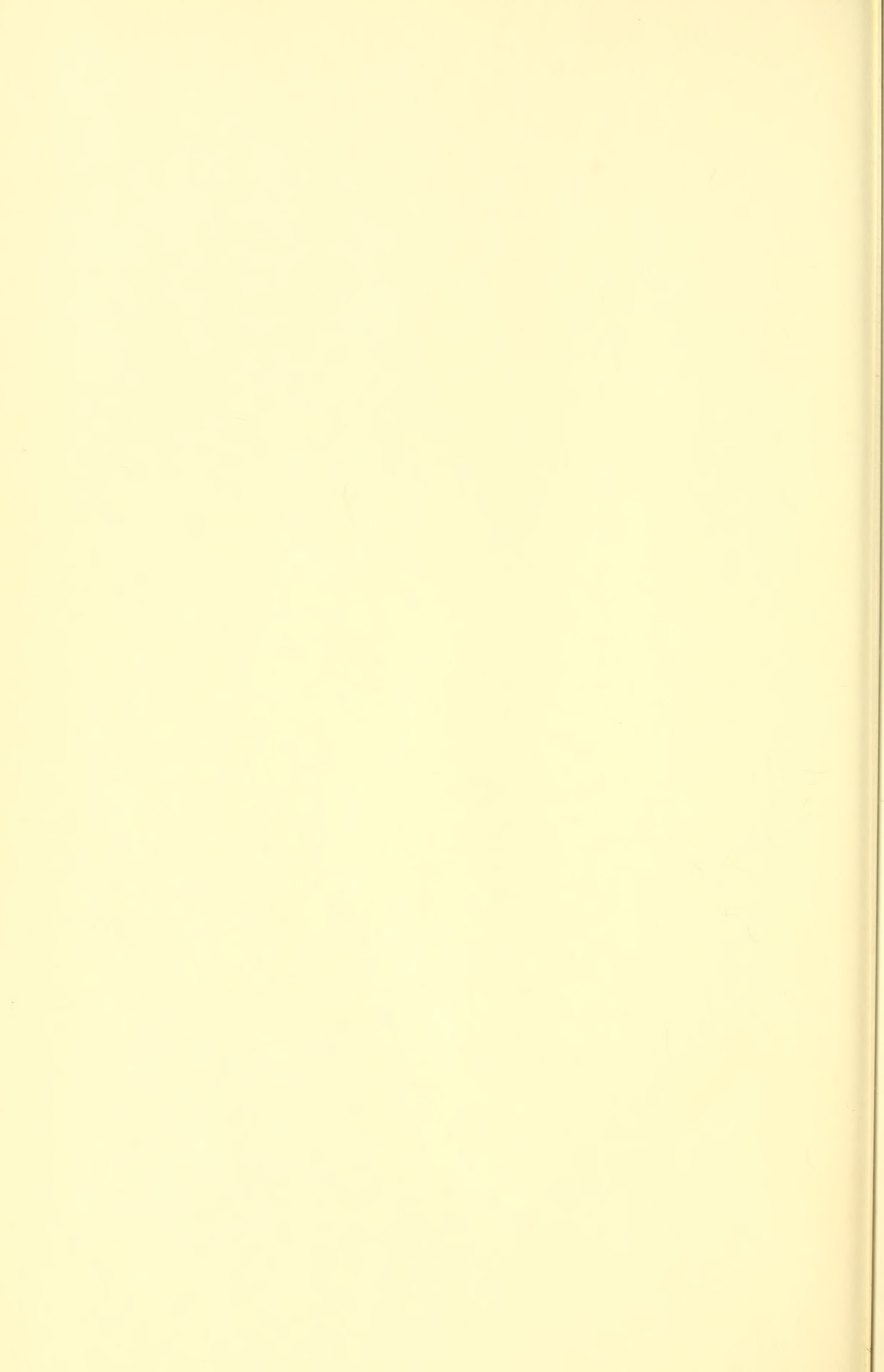
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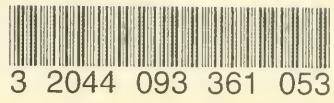
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